FOREST Science

A QUARTERLY JOURNAL OF RESEARCH AND TECHNICAL PROGRESS

Volume 5 - Number 4 - December - 1959

PUBLISHED BY SOCIETY OF AMERICAN FORESTE

WASHINGTON, D. C

FOREST SCIENCE is published quarterly by the Society of American Foresters with the cooperation of forestry research and educational organizations.

The journal assumes no responsibility for the statements and opinions expressed by contributors. The editors cannot be responsible for loss or damage of manuscripts and accompanying matter.

Correspondence concerning manuscripts submitted for publication and other editorial matters should be addressed to Prof. Stephen H. Spurr, School of Natural Resources, University of Michigan, Ann Arbor, Michigan.

Other correspondence, including subscriptions, remittances, reprint orders, and inquiries concerning the status of manuscripts accepted for publication, should be addressed to the Society of American Foresters, Mills Building, Washington 6, D. C.

Subscription price is $6.00 per year for complete volumes (one per calendar year), and $2.00 for single number. Add $0.25 for postage to Canadian addresses and $0.50 for postage to other foreign addresses.

The pages of FOREST SCIENCE are open to all qualified contributors. Preference will be given to papers devoted to the presentation and discussion of the results of original research. Authors are expected to bear the cost of that portion of their papers in excess of 16 printed pages in length and of tabular and illustrative material constituting more than 20 percent of the length of the paper.

Papers of 32 printed pages or longer (approximately 20,000 words or about 65 pages of manuscript) will be considered for publication as *Forest Science Monographs* under the same editorial procedures followed for shorter contributions. The monographs will be printed with covers, distributed without charge to the subscribers as supplements to regular issues, listed in the table of contents of the appropriate issue of FOREST SCIENCE, and included in the annual index. The entire cost of printing and mailing each monograph (but not editorial costs) must be met by the author or other agency.

Board of Edito

Stephen H. Spu
Edit
School of Natural Resour
University of Michig

Henry Clepp
F. H. Eyr
Society of American Foreste

V. L. Harp
Forest Service, U. S. Department of Agricultur

Business Manag

Miss L. Audrey Warr
Society of American Foreste

Copyright, 1959, by the Society of American Foreste

Second class postage paid at Washington, D. C., and at additional mailing offi

Printed in the United States of Amer

FOREST *Science*

A Quarterly Journal of Research and Technical Progress

Root Regeneration of Ponderosa Pine Seedlings Lifted at Different Times of the Year
Edward C. Stone, Gilbert H. Schubert 322

Seasonal Discoloration of Scotch Pine in Relation to Microclimatic Factors
H. D. Gerhold 333

Distribution of Organic Matter and Plant Nutrients in a Plantation of Scots Pine
J. D. Ovington, H. A. I. Madgwick 344

Brooming Response of Black Spruce to Dwarfmistletoe Infection
Ralph L. Anderson, F. H. Kaufert 356

Natural Emplacement of Dwarfmistletoe Seed on Ponderosa Pine
Lewis F. Roth 365

Bias Due to Edge Effect in Using the Bitterlich Method
Toshiro Haga, Kanjiro Maezawa 370

The Secondary Phloem of Douglas-Fir
Steve J. Grillos, Frank H. Smith 377

Influence of the Seed Coat on Germination, Water Absorption, and Oxygen Uptake of Eastern White Pine Seed
Theodore T. Kozlowski, Arthur C. Gentile 389

Some Sampling Attributes of the Negative Binomial Distribution With Special Reference to Forest Insects
W. E. Waters, W. R. Henson 397

REVIEWS: Economics of American forestry 355; Methods of vegetation study 364; Forest fire: control and use 395; Apical meristem aging and silviculture 412.

Advisory Board

Harry A. Fowells
Scott S. Pauley
Carl H. Stoltenberg
John A. Zivnuska

F. Paul Keen
François Mergen
J. Harry G. Smith
Donald P. White

George H. Hepting
T. T. Kozlowski
Leslie W. Orr
Robert Zahner

Volume 5
December 1959
Number 4

Root Regeneration by Ponderosa Pine Seedlings Lifted at Different Times of the Year

BY
EDWARD C. STONE
GILBERT H. SCHUBERT

CALIFORNIA has had an organized forest planting program since 1910. Yet in nearly 50 years less than 75,000 acres have been planted. Planting has been held back for many reasons the most important being poor seedling survival and an inability to explain why.

A popular explanation for poor survival has been the long dry season. Yet planting has succeeded many times. Perhaps Californians need not wait for the climate to change, but rather should search for suitable combinations of site preparation, lifting time, storage conditions, and planting techniques. For example, the data to be presented here indicates that lifting time must be considered because it exerts a significant influence on root regeneration.

The ability of a seedling to regenerate an extensive root system rapidly when transplanted is a critical factor in determining whether it will live or die. For example, a two-year-old ponderosa pine seedling has the "heterorhizic" root system typical of most conifers; it has a primary root, several elongated first or second order laterals, and many short first, second, third, and fourth order laterals varying in length from less than a sixteenth to an inch or more (Fig. 1; Noelle, 1910). When the seedling is dug for bare-root transplanting, most of the elongated laterals, the primary root, and several short laterals are broken off and left in the ground. When the seedling is replanted the roots soon exhaust available moisture in the surrounding soil unless the unbroken laterals elongate rapidly or new laterals form and grow rapidly. Without an actively elongating root system to tap new sources of moisture the seedling depends on moisture diffusing increasingly greater distances through the soil mass. Eventually, when the transpiration rate exceeds the rate of diffusion within the soil, the seedling dries out and dies.

Published studies on the root growth of trees and tree seedlings go back at least two hundred years although it is only during the last one hundred years that reports have appeared in a more or less

---

Stone is Associate Professor, School of Forestry, University of California, Berkeley. Schubert is Research Forester, Pacific S.W. Forest and Range Expt. Sta., U. S. Forest Service, Berkeley.

Joint project, Univ. of Calif. Agric. Expt. Sta. No. 1577, and Calif. Forest and Range Expt. Sta. Funds in support of this work were received in part from the California Division of Forestry and the U. S. Forest Service.

steady stream.[1]

Few of these reports agree completely, but most differences can be ascribed to the species or the particular climate involved. Speaking generally, it appears that: the root behavior of gymnosperms and angiosperms is not the same; root behavior varies among species within the same genus; there is a period of active root elongation in both the spring and the fall; and root elongation in the summer and winter may sometimes be due to an endogenous rhythm, at other times to environmental changes, for example, drought and low temperature.

Except for preliminary reports by Wakeley (1954), Stone (1955), and Stone and Schubert (1956), none of these investigations dealt with root growth on recently transplanted seedlings. Consequently the study reported here was considered a necessary step in the development of reliable planting systems for California. Although incomplete, the data appear of sufficient interest to justify their publication at this time.

Materials and Method

In essence the study was a simple one in which seedlings were dug from the nursery each month, replanted in the greenhouse, redug 30 days later, and examined for new roots.

Two-year-old (1-1) ponderosa pines were used in two series of tests. The first, in 1955-56, used seedlings grown from seed collected in the southern westside Sierra, or Zone V as described by Fowells (1946); the second series, 1956-57, from the northern westside Sierra or Zone III. Both lots of seed were planted and seedlings grown for the first year in seed beds at the U. S. Forest Service Mt. Shasta Nursery near McCloud, Calif. At the beginning of the second growing season Zone V seedlings were replanted in nearby transplant beds from which they were subsequently lifted and shipped to Berkeley. Because of the unfavorable lifting and shipping conditions experienced with this first series of seedlings, Zone III seedlings were replanted the second year

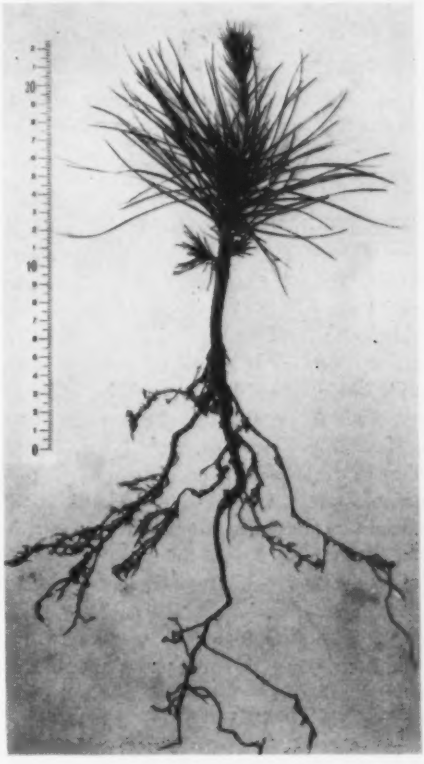


FIGURE 1. *Typical two-year-old ponderosa pine seedling, showing the "heterorhizic" root system (scale is in cm).*

[1]Duhamel, 1760; Mohl, 1862; Hartig, 1863; Resa, 1878; Rossow, 1884; Gulbe, 1888; Wieler, 1894; Peterson, 1898; Goebel, 1900; Hammerle, 1901; Busgen, 1901; Engler, 1903; McDougal, 1916; Harris, 1926; Crider, 1928; Stevens, 1931; Kinman, 1932; Laing, 1932; Woodroof and Woodroof, 1934; Heinicke, 1935; Collison, 1935; Ladefoged, 1939; Reed, 1939; Wilcox, 1954; Wakeley, 1954; Stone, 1955; Stone and Schubert, 1956; Richardson, 1958.

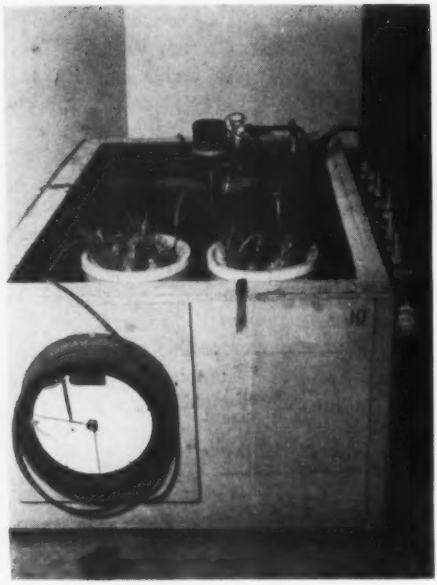


FIGURE 2. *Water bath with crocks, seedlings, and suction hoses used for drainage in place.*

in transplant beds at the Institute of Forest Genetics Nursery near Placerville, Calif. Thus the seedlings used in the two series were from different seed sources and during their second growing season were grown under different climates, Placerville having a milder climate and a longer growing season than McCloud.

Seedlings were dug on or about the first day of each month, packed in peat moss, shingle-tow, or vermiculite, and shipped by freight to Berkeley where they were immediately placed in cold storage at 1°C until used, occasionally as long as 4 or 5 days later. Just before planting, the roots were pruned to about 6 inches, and any white root tips still present were pinched off.

For the 1955-56 series, 10 seedlings were planted in each of 8 crocks filled with sand. Two crocks were then placed in each of four constant temperature water baths maintained at 10°C (50°F), 15°C (59°F), 20°C (68°F), and 25°C (77°F). Each crock was watered after planting and three times each week thereafter with 1/10-strength Hoagland's solution. The excess solution which drained to the bottom after each application was removed through an inverted glass thistle tube connected to a trap and a vacuum line (Fig. 2).

Thirty days after planting, the crocks were removed from the water baths and the seedlings carefully washed from the sand. The new roots which had just started to suberize, but which could still be recognized as new roots, were counted and those 0.5-inch and longer measured. The air temperature in the greenhouse did not fall below 20°C (68°F) at night, and with but few exceptions did not exceed 35°C (95°F) in the daytime. Thus the seedling roots were exposed to a constant temperature, an abundant supply of moisture and nutrients, and the top was exposed to a varying air temperature and a changing photo-period.

The 1956-57 series was handled in the same fashion except that sponge-rock was substituted for the sand.

Results

The root system was regenerated by elongation of short laterals present at the time the seedling was transplanted and by initiation and elongation of new laterals (Figs. 3 to 6). Seedlings from Zone III seed grown at Placerville behaved differently than seedlings from Zone V seed grown at the Mt. Shasta Nursery, but both groups showed a pronounced seasonal periodicity in lateral root elongation and initiation.

Lateral root elongation on seedlings from both zones occurred from September to June and was absent or of a limited nature from June to September (Fig. 7). The peak elongation occurred on Zone III seedlings in March and on Zone V seedlings 2 months later in May (Fig. 7). At these peak periods, 100 percent of the Zone III seedlings showed lateral root

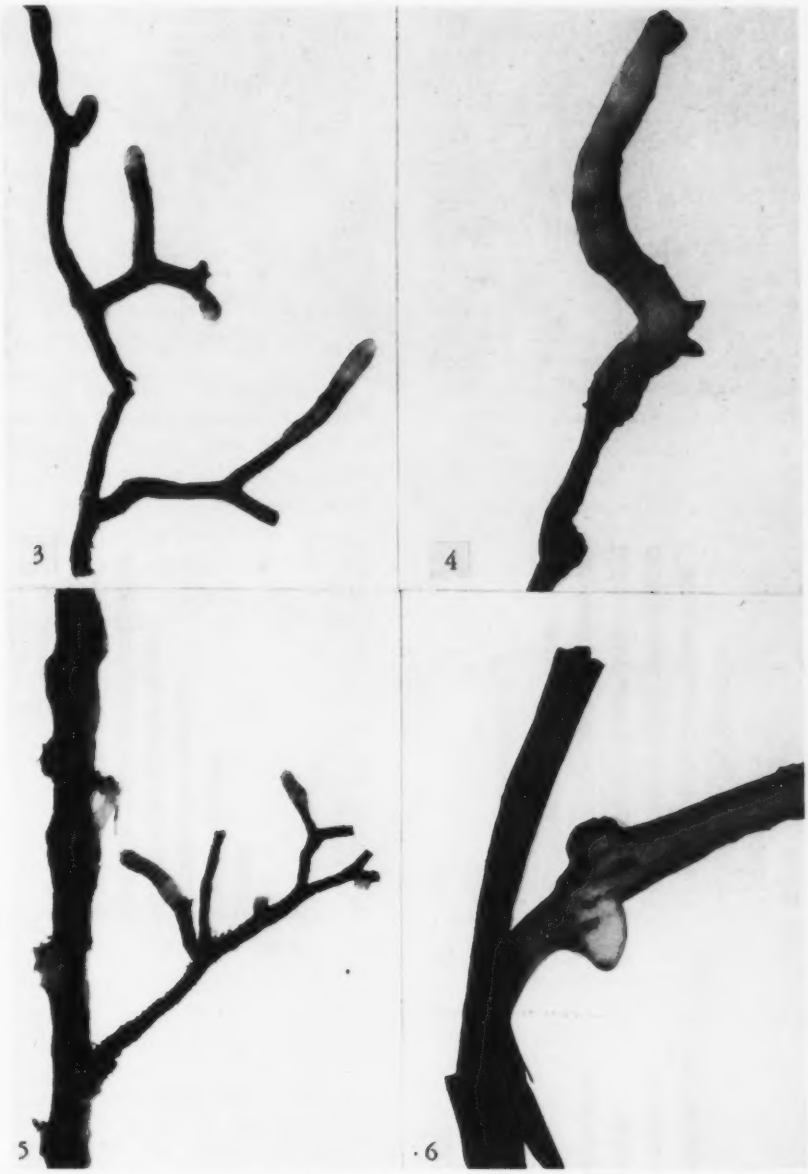


FIGURE 3. *Part of the root system showing lateral branching,* × 7. *Lighter colored tips indicate active elongation.* FIGURE 4. *An elongating lateral root,* × 5½. *The lighter colored part is new growth.* FIGURE 5. *Part of the root system showing both lateral root elongation and lateral root initiation,* × 7. *The branched tips to the right are actively elongating; the light spots at the left are recently initiated laterals.* FIGURE 6. *Short length of root with bark peeled away to show recently initiated lateral root,* × 7.

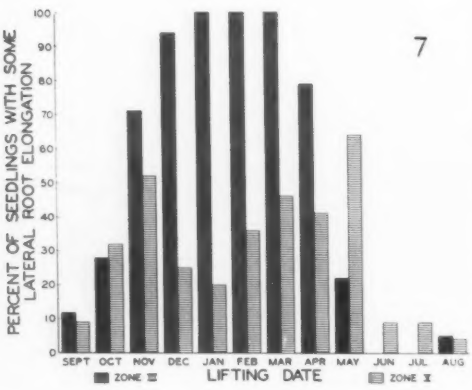
elongation averaging 67 per seedling, and 64 percent of the Zone V seedlings showed lateral root elongation averaging 23 per seedling (Figs. 7 and 8).

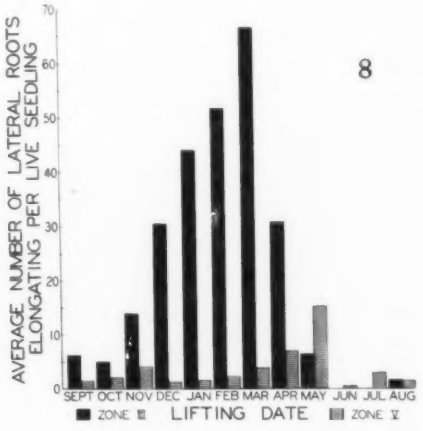
Lateral root initiation was also evident from September to June, but was prominent only from December to May on Zone III seedlings and only during April and May on Zone V seedlings (Fig. 9).

Soil temperature influenced the number of new lateral roots initiated, the number of lateral roots already present that resumed growth, and the amount of lateral root elongation after the seedling had been transplanted to the greenhouse (Tables 1-3).

Root initiation on Zone III seedlings was apparent at 25°C and 20°C only from September through April, at 15°C only from November through April, and at 10°C only during March (Table 1). Root initiation on Zone V seedlings was only apparent in the spring—during April and May at 25°C, during April, May and June at 20°C, and during April and May at 15°C and 10°C (Table 1). For both zones and at all soil temperatures initiation was most evident in the spring (Table 1).

Throughout the year some lateral roots of Zone V seedlings resumed growth within 1 month after transplanting, provided





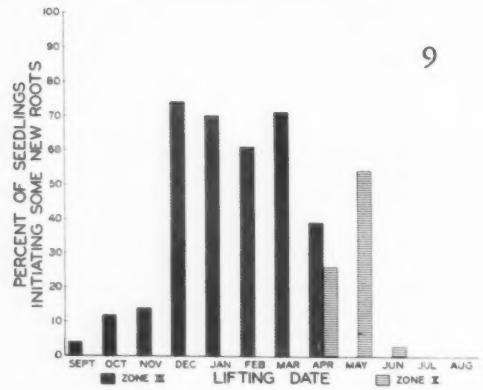


FIGURE 7. *Percent of seedlings that showed some lateral root elongation within one month after being transplanted to the greenhouse.* FIGURE 8. *Average number of lateral roots per live seedling that showed some elongation within one month after being transplanted to the greenhouse.* FIGURE 9. *Percent of seedlings showing root initiation within one month after being transplanted to the greenhouse.*

the soil temperature was maintained at either 20°C or 25°C (Table 2). At 15°C no roots elongated during August, and at 10°C none from June to December. The greatest number of lateral roots elongated when the soil temperature was held at 20°C (Table 2). Zone III seedlings behaved differently. At 25°C no roots elongated during June and July, at 20°C and 15°C none from June through August, and at 10°C none from May through October (Table 2). At soil temperatures of 20°C and 25°C the number of elongating roots was not significantly different even though at 20°C there was no elongation in August while there was some at 25°C (Table 2). At 15°C there was a significant reduction in the number and at 10°C a still further significant reduction (Table 2).

The amount of lateral root elongation on seedlings from both zones varied directly with the soil temperature (Table 3). At 25°C the total length of elongated roots was 2-3 times as great as at 20°C, which in turn was 3-5 times as great as at 15°C, which in turn was 50-100 times as great as at 10°C. (Table 3).

TABLE 1. Number of seedlings showing root initiation and the number initiated within one month after transplanting to controlled temperature baths.[1] *(Seed Zone V seedlings were grown at the Mt. Shasta Nursery 1955-56; seed Zone III seedlings were grown at the Placerville Nursery 1956-57).*

Month transplanted	Zone	10°C		15°C		20°C		25°C		Total[2]	
		Seedlings	Roots	Seedlings	Roots	Seedlings	Roots	Seedlings	Roots	Seedlings	Roots
					Number						
Sept.	V	0	0	0	0	0	0	0	0	0	0
	III	0	0	0	0	2	45	1	40	3	85
Oct.	V	0	0	0	0	0	0	0	0	0	0
	III	0	0	0	0	7	50	2	45	9	95
Nov.	V	0	0	0	0	0	0	0	0	0	0
	III	0	0	1	5	6	60	4	50	11	115
Dec.	V	0	0	0	0	0	0	0	0	0	0
	III	0	0	19	335	20	625	20	590	59	1550
Jan.	V	0	0	0	0	0	0	0	0	0	0
	III	0	0	16	445	20	770	20	725	56	1940
Feb.	V	0	0	0	0	0	0	0	0	0	0
	III	0	0	10	200	19	450	20	705	49	1355
March	V	0	0	0	0	0	0	0	0	0	0
	III	11	115	14	175	18	295	14	195	57	780
April	V	2	10	6	90	9	360	4	80	21	540
	III	0	0	14	360	7	225	10	260	31	845
May	V	5	25	14	365	12	420	12	160	43	970
	III	0	0	0	0	0	0	0	0	0	0
June	V	0	0	0	0	2	60	0	0	2	60
	III	0	0	0	0	0	0	0	0	0	0
July	V	0	0	0	0	0	0	0	0	0	0
	III	0	0	0	0	0	0	0	0	0	0
Aug.	V	0	0	0	0	0	0	0	0	0	0
	III	0	0	0	0	0	0	0	0	0	0
Total[3]	V	7	35	20	455	23	840	16	240	66	1570
	III	11	115	74	1520	99	2520	91	2610	275	6765

[1]Twenty seedlings per treatment for each zone.

[2]For Zone V a difference between month totals greater than 6 for seedlings and 137 for roots and for Zone III a difference greater than 8 and 218 is significant at the 95 percent level of probability.

[3]For Zone V a difference between temperature totals greater than 10 for seedlings and 236 for roots and for Zone III a difference greater than 14 and 378 is significant at the 95 percent level of probability.

TABLE 2. Number of live seedlings, number of seedlings with some lateral root elongation, and number of lateral roots that elongated within one month after transplanting to controlled temperature baths.[1] *(Seed Zone V seedlings were grown at the Mt. Shasta Nursery, 1955-56; seed Zone III seedlings were grown at the Placerville Nursery 1956-57.)*

Month transplanted	Zone	10°C			15°C			20°C			25°C			Total[2]		
		Live seedlings	Seedlings with some roots elongated	No. of elongated roots	Live seedlings	Seedlings with some roots elongated	No. of elongated roots	Live seedlings	Seedlings with some roots elongated	No. of elongated roots	Live seedlings	Seedlings with some roots elongated	No. of elongated roots	Live seedlings	Seedlings with some roots elongated	No. of elongated roots
		Number														
Sept.	V	20	0	0	19	1	2	17	4	61	11	2	30	67	7	93
	III	11	0	0	15	2	13	13	4	142	5	4	117	44	10	272
Oct.	V	20	0	0	20	17	72	20	9	93	20	9	56	80	35	221
	III	20	0	0	18	7	85	18	9	197	12	6	60	68	22	342
Nov.	V	20	0	0	20	14	70	20	12	125	20	16	129	80	42	324
	III	20	1	10	20	20	444	18	18	318	18	18	283	76	57	1055
Dec.	V	20	2	2	20	7	50	18	9	29	16	2	12	74	20	93
	III	20	15	141	20	20	698	20	20	797	20	20	798	80	75	2434
Jan.	V	20	2	2	14	7	37	9	5	22	5	2	4	48	16	65
	III	20	20	648	20	20	714	20	20	905	20	20	1255	80	80	3522
Feb.	V	20	4	10	19	10	41	18	8	67	20	7	56	77	29	174
	III	20	20	502	20	20	1163	20	20	1475	20	20	1005	80	80	4145
Mar.	V	17	5	6	18	11	48	18	13	143	20	8	87	73	37	284
	III	20	20	691	20	20	1107	20	20	1583	20	20	1947	80	80	5328
Apr.	V	19	6	15	19	10	67	18	10	362	17	7	68	73	33	512
	III	20	11	60	20	16	497	20	18	987	20	18	929	80	63	2473
May	V	19	10	45	19	15	188	18	14	445	19	12	470	75	51	1148
	III	19	0	0	17	10	165	14	5	156	5	3	33	55	18	354
June	V	15	0	0	19	3	3	18	2	14	11	2	10	63	7	27
	III	9	0	0	0	0	0	1	0	0	0	0	0	10	0	0
July	V	13	0	0	9	1	9	5	1	1	8	5	100	35	7	110
	III	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aug.	V	20	0	0	20	0	0	16	1	2	12	2	10	68	3	12
	III	18	0	0	19	0	0	17	0	0	14	4	115	68	4	115
Total[3]	V	223	29	80	216	96	587	195	88	1364	179	74	1032	813	287	3063
	III	197	87	2052	189	135	4886	181	134	6560	154	133	6542	721	489	20040

[1]Twenty seedlings per treatment for each zone.

[2]For Zone V a difference between month totals greater than 7 for live seedlings, greater than 10 for seedlings with roots, and greater than 166 for elongated roots; and for Zone III a difference greater than 9, 7, and 494 is significant at the 95 percent level of probability.

[3]For Zone V a difference between temperature totals greater than 13 for live seedlings, greater than 18 for seedlings with roots and greater than 288 for elongated roots and for Zone III a difference greater than 15, 12 and 856 is significant at the 95 percent level of probability.

TABLE 3. Number of lateral roots that elongated 0.5 inch or more and the total root elongation on seedlings within one month after transplanting to controlled temperature baths.[1] *(Seed Zone V seedlings were grown at the Mt. Shasta Nursery 1955-56; seed Zone III seedlings were grown at the Placerville Nursery 1956-57).*

Month transplanted	Zone	10°C		15°C		20°C		25°C		Total	
		No.	Length (In.)	No.	Length (In.)	No.	Length (In.)	No.	Length (In.)	No.	Length (In.)[2]
Sept.	V	0	0	0	0	4	2.5	7	7.3	11	9.8
	III	0	0	0	0	24	18.7	58	78.7	82	97.4
Oct.	V	0	0	23	24.5	20	15.0	24	24.3	67	63.8
	III	0	0	2	1.0	29	20.6	16	11.9	47	33.5
Nov.	V	0	0	13	9.5	31	27.0	48	52.0	92	88.5
	III	0	0	9	4.8	41	33.5	90	92.9	140	131.2
Dec.	V	1	0.6	2	1.3	1	0.6	0	0	4	2.5
	III	0	0	41	30.0	116	106.8	380	529.0	537	665.8
Jan.	V	0	0	7	4.4	7	4.3	0	0	14	8.7
	III	6	3.0	76	68.1	329	400.9	430	712.1	841	1184.1
Feb.	V	0	0	7	5.2	19	28.8	19	22.8	45	56.8
	III	0	0	147	116.9	339	379.1	274	382.4	760	878.4
March	V	0	0	10	9.5	25	37.3	22	22.1	57	68.9
	III	4	2.6	49	42.8	388	331.9	572	719.5	1013	1096.8
April	V	0	0	14	11.4	28	22.0	26	29.2	68	62.6
	III	0	0	11	10.8	190	151.3	332	325.3	533	487.4
May	V	0	0	7	4.1	94	80.5	190	208.0	291	292.6
	III	0	0	2	1.0	1	0.5	1	.5	4	2.0
June	V	0	0	2	1.2	3	1.9	2	1.3	7	4.4
	III	0	0	0	0	0	0	0	0	0	0
July	V	0	0	0	0	1	1.6	28	28.4	29	30.0
	III	0	0	0	0	0	0	0	0	0	0
Aug.	V	0	0	0	0	2	4.6	7	12.1	9	16.7
	III	0	0	0	0	0	0	30	45.1	30	45.1
Total[3]	V	1	0.6	85	71.1	235	226.1	373	406.5	694	705.3
	III	10	5.6	337	275.4	1457	1443.3	2183	2897.4	3987	4621.7

[1]Twenty seedlings per treatment for each zone.

[2]For Zone V a difference between month totals greater than 72 for number and 90 for length and for Zone III a difference greater than 74 and 100 is significant at the 95 percent level of probability.

[3]For Zone V a difference between temperature totals greater than 126 for number and 156 for length and for Zone III a difference greater than 128 and 172 is significant at the 95 percent level of probability.

First month survival of transplanted seedlings from both zones varied inversely with the soil temperature; as the temperature decreased the survival increased (Table 2). On the other hand, the number of live seedlings that produced roots was significantly lower at 10°C than at the other soil temperatures (Table 2).

Discussion

When this study started, data were not available on the origin of the roots that made up the new root system of the transplanted seedling although we had observed that elongation of a relatively few short lateral roots made up the major portion of this new root system. It was not until the study was well underway that lateral root initiation was noted. Consequently data on Zone V seedlings may be incomplete and data on Zone III seedlings may present a more reliable picture (Table 1).

Since lateral root elongation and lateral root initiation are at a maximum in the spring, some workers might wonder if root initiation was confused with root elongation when the new roots were counted. As far as we could observe, newly formed roots were not counted. One month in the

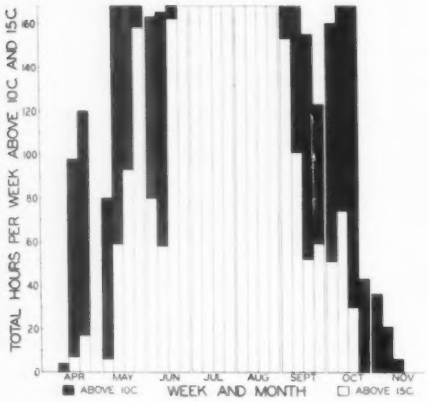


FIGURE 10. *Seasonal temperature pattern at the 7-inch soil depth during 1950 on an exposed south slope at elevation of 5,500 feet in the central Sierra Nevada.*

greenhouse was not long enough for the newly initiated lateral roots to protrude far enough through the bark to be recognized as new roots and be counted.

Only a relatively few short laterals, whether they were recently initiated or initiated before being lifted from the nursery, elongated rapidly and contributed to the development of the new root system. However, almost all short lateral roots, except mycorrhizal roots, retain the potential ability to elongate when the seedling is transplanted or the environment otherwise modified.

Nature of root initiation may explain to some extent why spring planting is often better than fall planting in California. Lifting, storing, shipping, and planting usually destroy many short lateral roots. In a thirty-day period when the soil temperature is 20°C or more spring-lifted seedlings will readily regenerate new laterals, some of which will then rapidly elongate; fall-lifted seedlings will regenerate few if any new laterals during the same period of time.

Some laterals resume growth during the first thirty days on both spring-lifted and fall-lifted stock, provided the soil temperature is maintained above 20°C. If the temperature is lowered to 10°C, then only the spring-lifted stock shows lateral root elongation. Even on spring-lifted stock root elongation is very slow at soil temperatures below 15°C. Consequently the expected seasonal soil temperatures should be considered when working out a planting plan.

For example Figure 10 shows the temperature pattern at the 7-inch depth on an exposed south slope at an elevation of 5,500 feet in the central Sierra during 1950. Soil temperatures were seldom above 10°C before the second week in April, and seldom above 15°C before the second week in May. Accordingly on this particular site during this particular year little if any root growth would have been evident before the middle of June on seedlings planted before the middle of May; on a north slope, root growth would have been even later. Often by this time the soil is considerably below field capacity and moisture stress becomes important.

Zone III and V stock showed significantly different behavior, but one must interpret this difference with caution. The data demonstrate that different lots of 2-year-old ponderosa pine seedlings can be expected to perform differently when field planted. What caused the difference in these two lots—the seed collection zone, the climate in which they were grown, the way they were lifted, the kind of temporary storage, the shipping conditions, or other factors? We cannot tell from the data.

Summary

Regeneration of a new root system by transplanted ponderosa pine seedlings is dependent, after root pruning, upon the elongation of the short laterals already formed and the initiation and elongation of new laterals.

Root elongation and root initiation of transplanted seedlings displayed a distinct seasonal periodicity. This periodicity was evident under greenhouse conditions where the soil moisture and nutrients were abundant, the soil temperature was held con-

stant, and the air temperature was not allowed to fall below 20°C (68°F) at night.

In general root elongation and root initiation did not occur on seedlings transplanted into the greenhouse in July and August. Root elongation was evident at all other times, but root initiation was evident only on seedlings transplanted from December to June; however the greatest activity was in the spring immediately before the terminal bud broke.

The data presented, although incomplete, suggest that the seed collection zone, the nursery in which the seedling is raised, or both affect the physiological condition of the seedling and its subsequent response when transplanted.

The physiological behavior of ponderosa pine seedlings when transplanted suggest that spring planting has more in its favor than fall planting. In the spring a greater number of the short laterals elongate per unit time than in the fall. Furthermore, since a large percentage of the spring-lifted seedlings initiate new laterals, replacement of those roots that dry out and are killed during spring transplanting is possible. Also, the seedling can regenerate a new root system at a lower soil temperature in the spring than in the fall.

Literature Cited

BÜSGEN, M. 1901. Einiges über Gestalt und Wachstumsweise der Baumwurzeln. Allg. Forst u. Jagd Zeitung. 77:273-278, 305-309.

COLLISON, R. C. 1935. Lysimeter investigations—IV. Water movement, soil temperatures, and root activity under apple trees. N. Y. Agric. Expt. Sta. Tech. Bul. 237. 31 pp.

CRIDER, F. J. 1928. Winter root growth of plants. Science 68:403-404.

DUHAMEL. 1760. Des semis et plantation des arbres, et de leur culture. 383 pp. Gregrin and Delatour, Paris.

ENGLER, A. 1903. Untersuchungen über das Wurzelwachstum der Holzarten. Mitteil. Schweiz. Centralanstalt forstl. Versuchsw. 7:247-317.

FOWELLS, H. A. 1946. Forest tree seed collection zones in California. Calif. Forest and Range Expt. Sta. Res. Note 51. 5 pp.

GOEBEL, K. 1900. Organographie der Pflanzen, II. 648 pp. G. Fischer, Jena.

GULBE, L. A. 1888. Uber die periodische Thätigkeit des Cambiums in den Wurzeln unserer Baüme. Jahrb. d. St. Petersburger Forstinstitutes 3:1-47.

HÄMMERLE, J. 1901. Uber die Periodizität des Wurzelwachstums bei Acer Pseudoplatanus. Beitr. zur wissen. Bot. 4:150-165.

HARRIS, G. H. 1926. The activity of apple and filbert roots especially during the winter months. Proc. Amer. Soc. Hort. Sci. 23:414-422.

HARTIG, T. 1863. Uber die Zeit des Zuwachses der Baumwurzel. Bot. Zeit. 21:286-287.

HEINICKE, A. J. 1935. Root growth in young apple trees made shortly before and after defoliation. Proc. Amer. Soc. Hort. Sci. 33:164-165.

KINMAN, C. F. 1932. A preliminary report on root growth studies with some orchard trees. Proc. Amer. Soc. Hort. Sci. 29:220-224.

LADEFOGED, K. 1939. Untersuchungen über die Periodizität im Ausbruch und Längenwachstum der Wurzeln bei einigen unserer gewöhnlichsten Waldbäume. Det. forstl. Forsøgsv. i. Danmark 16:1-256.

LAING, E. V. 1932. Studies on tree roots, Forestry Comm. Bul. 13. London. 73 pp.

McDOUGAL, W. B. 1916. The growth of forest tree roots. Amer. J. Bot. 3: 384-392.

MOHL, H. V. 1862. Einige anatomische und physiologische Bemerkungen über das Holz der Baumwurzeln. Bot. Zeitung 20:313-319, 321-327.

NOELLE, W. 1910. Studien zur vergleichenden Anatomie und Morpologie der

Koniferenwurzeln mit Rucksicht auf die Systematik. Bot. Zeit. 68:169-266.

PETERSEN, O. G. 1898. Nogle Undersøgelser over Träernes Rodliv. Oversigt over d. Kongelige Danske Videnskabernes Selskabs Forhandlinger.

REED, J. F. 1939. Root and shoot growth of shortleaf and loblolly pines in relation to certain environmental conditions. Duke Sch. of For. Bul. 4. 52 pp.

RESA, F. 1878. Untersuchungen über die Periode der Wurzelbildung, insbesondere bei den Holzgewächsen. Forstliche Blätter 15:321-331.

RICHARDSON, S. D. 1958. Studies of root growth in *Acer saccharinum* L. VII. Root growth and winter dormancy. Proc. Kon. Ned. Akad. Wetensch. Amsterdam (in press).

RUSSOW, E. 1884. Uber Tupfelbildung und den Inhalt der parenchymatischen Elemente der Rinde vor und während der Knospenaustriebes und Beginns der Cambiumthätigkeit in Stamm und Wurzel der einheimischen Lignosen. Sitzungsber. d. Naturforscher - Gesell. bei der Universität Dorpat. 6:350-389.

STEVENS, C. L. 1931. Root growth of white pine. Yale University School of For. Bul. 32. 62 pp.

STONE, E. C. 1955. Poor survival and the physiological condition of planting stock. For. Sci. 1:90-94.

STONE, E. C. and G. H. SCHUBERT 1956. New roots on pine seedlings. Calif. Agric. 10:11, 14.

WAKELEY, P. C. 1954. Planting the southern pines. U. S. Dept. Agric. Monogr. No. 18. 233 pp.

WIELER, A. 1894. Uber die Periodizität in der Wurzelbildung der Pflanzen. Forstwiss. Centralblatt 16:333-349.

WILCOX, H. 1954. Primary organization of active and dormant roots of noble fir, *Abies procera*. Amer. J. Bot. 41:812-821.

WOODROOF, J. G. and N. C. WOODROOF. 1934. Pecan root growth and development. J. Agric. Res. 49:511-530.

Seasonal Discoloration of Scotch Pine In Relation to Microclimatic Factors

BY
H. D. GERHOLD

THE INCREASING popularity of plantation-grown Scotch pine (*Pinus sylvestris* L.) for Christmas trees has again drawn attention to the undesirable discoloration of this species in the autumn (Bramble and Cope, 1947; Stutzman, 1954; Nodwell, 1955). European foresters have long recognized that some races have a greater tendency to discolor than do others. But the cause of the loss in green color is not yet well understood, despite the numerous investigations carried out in the past 120 years.

The present study was undertaken to measure quantitatively the effects of several environmental factors and to determine their influence on the discoloration process. The factors studied were light intensity and quality, temperature, relative humidity, and daylength. A number of possible relationships are suggested by Figure 1. To test whether these are actual or chance correlations, groups of trees in four experiments were exposed to identical environmental conditions, with the exception of one or two factors which were artificially modified for study. Thus the resulting changes in needle color could be ascribed to the factor or factors being varied.

Review of Literature

Mohl (1837) first described the seasonal discoloration of Scotch pine and other evergreens. His external observations and microscopic studies were followed by other more intensive investigations which in general agree on the nature of intracellular changes that account for the change in needle color. In the autumn the tips of needles discolor first and to the greatest degree, while the color of basal portions changes less or not at all. The upper side turns bright yellow, while the lower side does not discolor as much. Needles at the tips of branches become more yellow than those farther back (Kraus, 1872; Haberlandt, 1876a; Engler, 1913). Chloroplasts move inward from the cell walls and congregate around the nucleus, with this process starting within cells in the center of the needle and progressing outward (Zacharowa, 1929).

In *Picea* a similar process takes place in darkness as well as in light (Lewis and Tuttle, 1920; 1923). As this gradual process continues, chloroplasts are disrupted and disappear altogether, their contents diffusing into the protoplasm (Kraus, 1872; Haberlandt 1876a; Zacharowa, 1929), although discoloration can occur without disruption of the chloroplasts (Schimper, 1885). In mid-winter, the protoplasm in the palisade cells is granular and is colored

---

The author is Instructor in Forestry at the Pennsylvania State University. This paper is part of a dissertation prepared under the guidance of Prof. François Mergen and submitted in 1958 to the Graduate School of Yale University in partial fulfillment of the requirements for the Ph.D. degree. It was authorized for publication on October 10, 1958, as Paper No. 2301 in the Journal Series of the Pennsylvania Agric. Expt. Sta. Portions of this study were conducted as part of a Northeast Regional Project (NE 27), a cooperative study involving agricultural experiment stations in the Northeastern Region and supported in part by regional funds, U. S. Dept. of Agriculture.

yellow-green by chloroplast pigments, while cells in the spongy mesophyll are affected less or not at all (Kraus, 1872; Haberlandt, 1876a). In the spring the diffused chlorophyll disappears and chloroplasts again assume their regular arrangement (Zacharowa, 1929).

There is considerable disagreement as to the time of year when discoloration begins. Depending on the authors, the dates range from early September to early December (compare with Fig. 1).

No doubt much of this variation can be attributed to differential effects of races and local climatic conditions. Without exception, the authors agree that the degree of yellowing increases until late winter or early spring, and that the green color suddenly returns in the spring (Kraus, 1872; Haberlandt, 1876a; Engler, 1913; Zacharowa, 1929; DenUyl, 1956). Similar discoloration patterns have been reported for *Pinus banksiana* Lamb. (Stoeckeler and Rudolf, 1956) and *Juniperus virginiana* L. (McDermott and Fletcher, 1955).

Mohl (1837) speculated about factors which might contribute to discoloration, the most obvious of which are exposure to sunlight and low temperatures. Subsequent investigations provided many facts about possible causes, but some facets of the phenomenon have yet to be completely explained.

Light intensity and quality. Shaded twigs stay green even on trees which otherwise discolor intensely (Engler, 1913), while portions exposed to strong sunlight discolor much more rapidly (Haberlandt, 1876a). Engler (1908) felt that strong insolation at high altitudes in Switzerland

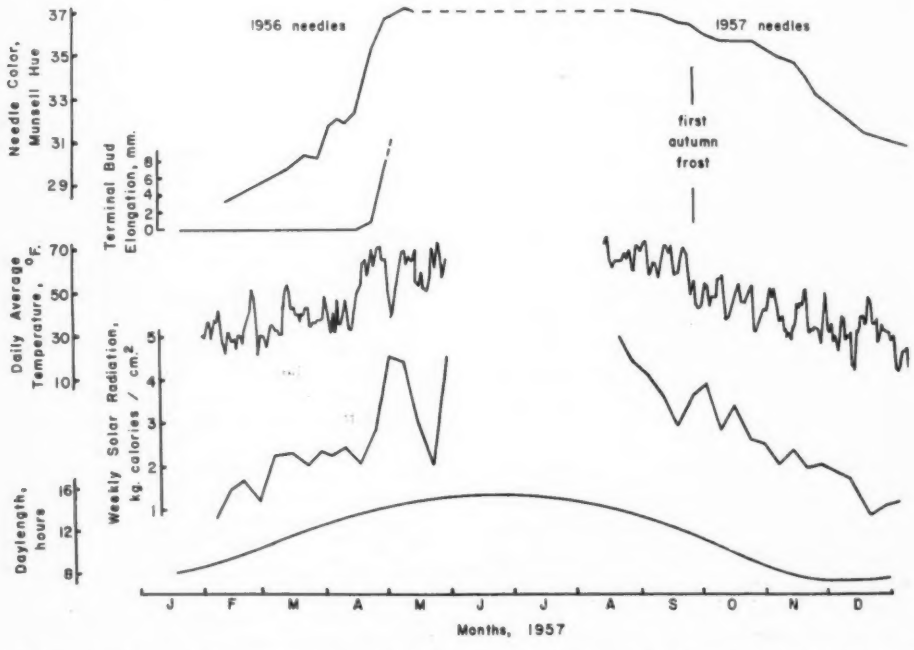


FIGURE 1. *Seasonal changes in the needle color of Scotch pine trees (seed source Austria) compared with climatic and phenotypic data collected near State College, Pennsylvania.*

accentuated winter discoloration. According to Lubimenko (1908), chlorophyll concentration in Scotch pine increases with decreasing light intensity until a maximum is attained, after which it diminishes. It has been established that intense light bleaches chlorophyll, both *in vitro* and in living plants (Askenasy, 1867; Wiesner, 1876; Pringsheim, 1881). Aronoff and Mackinney (1943) determined that the photooxidation of chlorophyll in benzene solution is a second order reaction with a low quantum efficiency, and noted a protective action of carotene.

While only indirect evidence is available to suggest the wavelengths of light that destroy chlorophyll, they are probably the same as those effective in photosynthesis (Rabinowitch, 1945; 1956). Wiesner (1876) allowed etiolated pea seedlings to become green in different wavelengths of light. At low intensities yellow light was most effective and blue least, while at higher intensities the order was reversed. He concluded that chlorophyll in nature is destroyed and formed simultaneously at certain intensities.

Guthrie (1929), working with soybean and sunflower plants, reported a decrease in chlorophyll when blue light was eliminated, and an increase when red light was eliminated. Yet Rudolph (1933), using bean plants, found that chlorophyll was formed mostly in red light, moderately in yellow-green, and slightly in blue, with the order reversed for carotenoids. The amount of chlorophyll formed in etiolated seedlings after a one second exposure to white light was almost as large as that formed after 600 seconds. Results of Sayre (1928) agree with those of Rudolph on the efficacy of various spectral regions in the formation of chlorophyll. Hacskaylo and Goslin (1957) covered Riga Scotch pines with black, blue, red, and colorless polyethylene, and observed that only those covered with red appeared to retain their green color from September to December.

Temperature. Kraus observed that leaves on which frost formed were the only ones discolored (1872), and that changes in chloroplast structure and color accompanied the first autumn frost (1874). He concluded that low temperature and not light is responsible for the discoloration because color is restored when leaves are exposed to elevated temperatures for several days (also Askenasy, 1867; Batalin, 1874; and Engler, 1913). This argument was refuted by Wiesner (1876), Haberlandt (1876a), and Schimper (1885), who agreed that while low temperatures do prevent or limit the formation of chlorophyll, light is the agent of destruction.

It appears that while the beginning of discoloration is not dependent on frost (Kienitz, 1911; 1922), low temperature is a contributing factor. Chlorophyll formation is known to be retarded at low temperatures (Lubimenko and Hubbenet, 1932). Haberlandt (1876b), upon exposing leaves to low temperatures under a microscope, noticed that the chloroplasts were damaged at $-4°$ to $-6°$C, and disruted at $-12°$ to $-15°$C. He and Kraus (1872) suggested that cold makes protoplasm more permeable and permits detrimental substances to reach the chlorophyll, possibly organic acids that are produced in the conversion of starch to oil. Engler (1913) felt that lowered temperatures cause decreased water absorption insufficient for transpirational needs, and therefore the discoloration is due to a lack of water.

Relative humidity. Only indirect references to a possible role of relative humidity in discoloration were found. Engler (1913) mentioned increased transpiration which accompanies strong insolation, in addition to decreased water absorption, as probable influences. Rudolph (1933) noted a beneficial effect of high humidity on chlorophyll formation in bean leaves. This information suggests that the maintenance of high relative humidity might reduce discoloration.

TABLE 1. Light intensity in the shading treatments.

Treatment	Incident light (percent of full sunlight)
Control, no shade	100
Clear plastic	75
Light shade	63
Medium shade	34
Heavy shade	13

Photoperiod. Wettstein (1954) noticed that when Scotch pine trees were exposed to artificially shortened photoperiods during the growing season, their needles discolored prematurely in September. A somewhat different mechanism appears to operate in soybeans and sunflowers, in which chlorophyll content decreases in response to increased daylength (Guthrie, 1929). A photoperiodic effect on the discoloration of Scotch pine is not unlikely, since photoperiod controls the cessation of cambial activity (Wareing, 1951), as well as other physiologic processes (Karschon, 1949; Wareing, 1950; Vaartaja, 1954; Echols, 1958).

There is considerable evidence to support a theory of photoperiodic ecotypes in this species, with continuous variation in thermoperiodic adaptation to the photoclimate of their environment (Engler, 1913; Langlet, 1942-3; Karschon, 1949; Vaartaja, 1954).

Experimental Procedures and Results

Four experiments were conducted to test the effects of environmental factors on Scotch pine discoloration. Trees of either one or two races were utilized in each study. Both of these races discolored considerably under ordinary fall and winter conditions. They differed in age and probably also in seed source. The larger trees had completed seven growing seasons and originated from Austria. The origin of the other trees, aged two to three years, is unknown.

Munsell Color Charts (1952) were used for periodic evaluations of needle color at a point one-third of the distance from the tip to the base of the needles. Only "Hue"[1] values were utilized in computations; recorded notations for "Value" and "Chroma" were disregarded in the analysis. The range of "Hue" values that were encountered extended from 25.0 ("Yellow") to 37.5 ("greenish Green-Yellow"). Results were subjected to analysis of variance.

Experiment A. The course of discoloration under five light intensities was followed from September 4 until October 26, 1956. Two-year-old Scotch pine trees growing in pots were assigned at random to each treatment. In four of the treatments, light intensity was reduced by placing the trees under a clear plastic roof that had been sprayed with aluminum paint; trees in the fifth treatment were exposed to full sunlight. Light intensities were measured with an incident light meter (Table 1). Maximum and minimum temperatures were recorded under each treatment and were found to be similar for all treatments.

Reductions in light intensity resulted in decreased needle discoloration (Fig. 2). Treatment effects were very highly significant, despite considerable individual tree variation. Differences among treatments were already evident on September 11 after seven days under treatment. The first autumn frost occurred on September 19. The treatment effects gradually increased in magnitude until the experiment was terminated on October 26. The discoloration of trees under heavy shade was so slight that it was difficult to distinguish visually. Since discoloration was already underway

[1]In the Munsell system of color notation, "Hue" indicates one of the five principal chromatic colors (red, yellow, green, blue, and purple); "Value" indicates the degree of lightness or darkness; and "Chroma" indicates the degree of departure of a particular Hue from a neutral gray of the same Value.

at the start of the experiment, it might have been possible to reduce it still further by an earlier and more complete protection against sunlight.

Experiment B. The relative effectiveness of various portions of the visible spectrum in causing discoloration was tested during the period August 29 to November 21, 1957. Clear and color-coated cellulose acetate sheets, 0.0075 inch thick, were made into sleeves and fitted over twigs in the upper two whorls of seven-year-old Scotch pine trees. Figure 3 shows light transmitted by the clear, blue, green, red, and yellow plastics, and for comparison the main peaks at which chlorophylls a and b absorb light are also given.

Four trees, one in each of four blocks, were randomly assigned to each of the five color treatments; there were eight plastic sleeves per tree, each of them applied for a different period of time (Table 2).

All plastics, including the clear, were effective in reducing discoloration of seven-year-old Scotch pine trees (Fig. 4). Part of their effect can be attributed to factors other than light quality, namely temperature. The effect of the blue and the yellow plastics could not be separated statistically from that of the clear plastic. Red

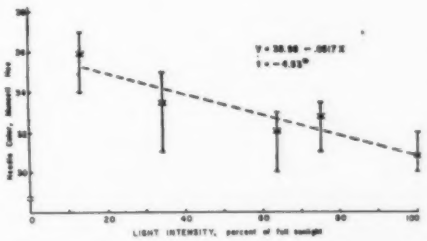


FIGURE 2. *Influence of incident light intensity on discoloration of two-year-old Scotch pine trees, showing the average and the range of needle colors on October 26 resulting from treatments imposed on September 4, 1957.*

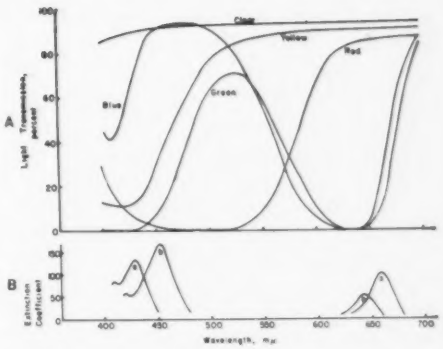


FIGURE 3. *A. Light transmitted by the clear and colored plastics. B. Position of absorption peaks of chlorophylls a and b in ether solution. Transmission measurements were made with a "G.E." recording spectrophotometer.*

was significantly higher than clear, blue, and yellow; and green was significantly higher than red. Differences in transmitted light intensity are insufficient to explain their significant effects on discoloration. Duration of treatments had a very highly significant effect on needle color, the effectiveness in protecting green color increasing with the length of treatment. The low values obtained for the green and blue plastics for the ten week treatment can be partially explained by the fact that these colors faded noticeably. Values in the first period of treatments were somewhat lower than those in the second period, and the difference approached significance at the five percent level.

Experiment C. Effects on discoloration by uniformly high, uniformly low, and fluctuating relative humidities, along with protection against freezing temperatures, were studied from September 6, 1956, to March 30, 1957. Two-year-old trees in pots were randomly assigned to seven treatment groups. In six of the groups, the above-ground portions of six trees were completely enclosed with clear waterproof

TABLE 2. Periods during which Scotch pine twigs on each tree were enclosed in plastic sleeves.

Date applied	Date removed	Duration in weeks
Period 1 (Aug. 29 to Nov. 7)		
Aug. 29	Sept. 26	4
Aug. 29	Oct. 10	6
Aug. 29	Oct. 26	8
Aug. 29	Nov. 7	10
Period 2 (Sept. 13 to Nov. 21)		
Sept. 13	Nov. 21	10
Sept. 26	Nov. 21	8
Oct. 10	Nov. 21	6
Oct. 26	Nov. 21	4

plastic sheets. One group was left uncovered as a control. A heating coil was used to maintain air temperatures above 6°C for three of the groups; the others were exposed to normal temperatures. Ammonium monophosphate solution kept relative humidity above 90 percent in two of the groups; calcium chloride, changed when necessary, maintained low relative humidity in two other groups; and in the three remaining groups relative humidity was not controlled and fluctuated widely.

The wide range in relative humidities had no apparent effect on the discoloration of Scotch pine, but protection against freezing temperatures reduced the yellowing (Fig. 5). The difference in needle color resulting from protection against freezing temperatures, as compared to trees not receiving this protection, was significant at the 0.1 percent level. The former were actually greener in color on March 30 than on November 19, while trees in the latter category were more yellow. A significant interaction between humidity and protection against freezing temperatures was revealed by the analysis of variance. It is believed that this can be attributed to changes in light and temperature as a result of water condensing inside the plastic covers enclosing the high humidity treatments. The condensed water would act to reduce the intensity of sunlight during the day, and would also reduce the loss of heat at night by filtering out long wave radiation.

Experiment D. Photoperiodic and thermal effects on discoloration were tested in combination from August 13 to December 12, 1957. Three-year-old trees in pots and seven-year-old trees in plastic-lined containers were assigned at random to six treatments, three of each age per treatment. Long, natural, and short daylengths were administered under normal and elevated temperature regimes; the durations of photoperiods were 15 to 16 hours, 9⅓ to 13⅔ hours, and 8½ to 9½ hours, respectively. For the long-day treatment, natural photoperiods of central Pennsylvania were extended with supplemental light from a 100 watt incandescent bulb. Short day exposures were produced by covering the trees with plywood sheets to exclude light late in the day. One-half of the trees were kept in a greenhouse where temperatures were thermostatically main-

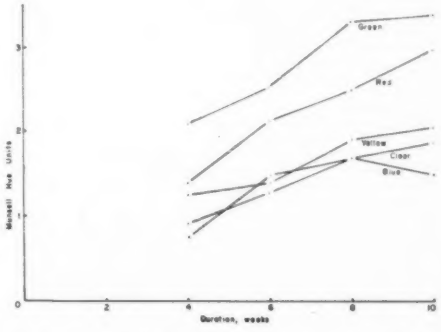


FIGURE 4. *Effectiveness of clear and colored plastics applied for different periods of time in reducing discoloration of seven-year-old Scotch pine trees. Values were obtained by subtracting the color of untreated needles from the color resulting from treatment.*

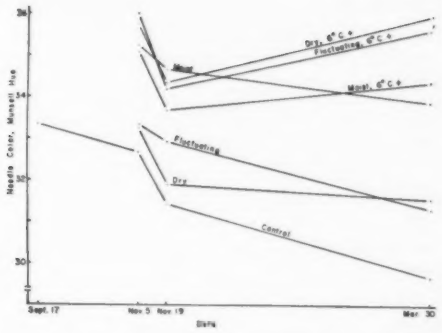


FIGURE 5. *Effects of relative humidity (moist, fluctuating, dry) along with protection against frost (6°C+) on discoloration of two-year-old Scotch pine trees.*

tained above 60°F, and rarely exceeded 85°F. The other trees were kept outside at normal temperatures.

Photoperiodic and thermal effects on the discoloration of seven-year-old Scotch pine trees are illustrated in Figure 6; chronological changes in statistical significance of effects of the two factors and their interaction are indicated in Table 3. Three-year-old trees reacted in a similar manner, but a comparison by age classes would not be valid as the effects of age and seed source are confounded. Under ordinary climatic conditions of central Pennsylvania, gradual discoloration was underway before August 28; from November 20 to December 12 it was very rapid.

Color changes in trees exposed to temperatures above 60°F were so slight that they could not be detected without color charts. Trees subjected to shortened daylengths, within both temperature regimes, discolored more severely than others during the period from late August until early October. The needle color of trees exposed to ordinary temperatures under prolonged daylengths remained green until early December, and was similar to the color of trees kept at temperatures above 60°F and at normal daylengths. After December they began to discolor slightly, but in an abnormal manner: green color began to fade evenly in all parts of the needles, and the tips and margins did not become yellow. Photoperiodic effects could be detected statistically by September 17, but thermal effects were not evident until October 2, after frosts had occurred during the nights of September 26, 27, and 28.

Discussion

By altering the magnitude or quality of climatic factors, either singly or in combination, it was demonstrated that light, temperature, and photoperiod play important roles in the seasonal discoloration of Scotch pine. No effect of relative humidity could be detected. The active factors may exert their influence on one or both of two processes which affect needle color: chlorophyll destruction, and chlorophyll synthesis.

Insolation is probably the most important single agency of chlorophyll destruction, because discoloration can be almost completely eliminated by decreasing the intensity of incident light, or filtering out the wavelengths of light absorbed by chlorophyll. The effect of light intensity appears

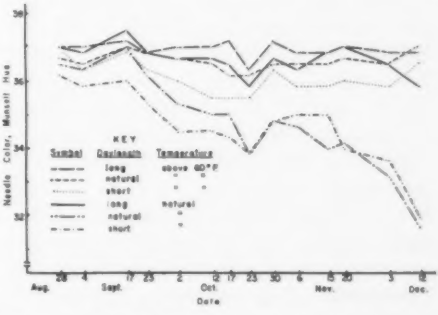


FIGURE 6. *Effects of temperature and daylengths on discoloration of seven-year-old Scotch pine trees. Results of same treatments on three-year-old trees were very similar.*

TABLE 3. Chronological changes in the F values from variance analyses of daylength and temperature effects on discoloration of seven-year-old Scotch pines.

Date	Source of variation		
	Daylength	Temperature	Daylength and temperature
Aug. 28	2.38	3.43	2.00
Sept. 4	5.85	1.92	0.31
Sept. 17	7.99*	0.82	2.99
Sept. 23	8.87*	5.40	1.40
Sept. 26		First autumn frost	
Oct. 2	12.32*	16.41*	1.95
Oct. 12	20.97**	16.51*	2.11
Oct. 17	10.49*	8.31*	0.23
Oct. 23	12.15*	37.38**	4.77
Oct. 30	28.32**	56.87**	5.05
Nov. 6	13.23*	27.78**	4.00
Nov. 15	13.90*	17.02*	7.45*
Nov. 20	25.08**	38.62**	12.40*
Dec. 3	12.67*	30.62**	6.17
Dec. 12	41.47**	291.51***	39.40**
Dec. 20	50.38**	69.42**	7.79**

*Significant at the 5 percent level.
**Significant at the 1 percent level.
***Significant at the 0.1 percent level.

to be linear above 13 percent (Fig. 2). It is likely that the most destructive wavelengths of light are in the vicinity of 450 mu; these were almost completely filtered out by the red and green plastics. The superiority of green plastic is probably due to its additional filtration near 650 mu.

This concept of chlorophyll destruction is not contrary to current knowledge (Rabinowitch, 1945; 1956), but neither is it sufficient to account for seasonal and racial aspects of discoloration. There are probably seasonal and racial differences in the rate of synthesis, or the rate of destruction, or both.

Chlorophyll synthesis is curtailed at low temperatures, and the optimum temperature varies among species (Lubimenko and Hubbenet, 1932; Larsen, 1950), but there are no reports of racial differences. Neither does the lower chlorophyll content of beans and soybeans in response to increased daylength (Guthrie, 1929) offer a means of explaining the situation in dormant Scotch pine.

Consideration of destructive effects of these factors on chlorophyll seems more fruitful, with two distinct possibilities presenting themselves. Kraus (1874) and Haberlandt (1876a) have suggested that the disrupting influence of frosts on chloroplasts and protoplasm may expose chlorophyll to decomposition by the acids involved in the conversion of starch to oils. Langlet (1936) has reported that fats accumulate as Scotch pines become dormant, which is a result of shortened photoperiod (Wareing, 1951) and low temperature (Tuttle, 1919).

A second mechanism by which chlorophyll could be destroyed may be proposed to explain the discoloration of Scotch pine. Rabinowitch (1945; 1956) cited several examples of photautoxidation of chlorophyll as a result of the inhibition of photosynthesis. In this process chlorophyll is

oxidized by the action of intense light when photosynthesis is suppressed by either narcotics or starvation. Freeland (1944) detected feeble photosynthesis in *Pinus sylvestris* during the winter at temperatures above −6°C. Thus in dormant Scotch pine, sunlight could destroy chlorophyll after photosynthesis has been curtailed by shortened photoperiod and low temperatures. The latter theory does not conflict with any results reported here, and is favored by the findings of Experiments A and B, which indicate that solar radiation is of major importance. But reduced synthesis of chlorophyll and its destruction by plant acids may also play important roles in discoloration.

The differential response of Scotch pine races to photoperiod (Karschon, 1949; Vaartaja, 1954) could explain why some races discolor intensely while others exposed to identical temperatures and solar radiation discolor very little. The former races become dormant sooner (Engler, 1913; Wettstein and Grüll, 1954), and store greater quantities of fats in their needles (Langlet, 1946).

It is tempting to speculate on the genetic survival value of the "protective coloration," as Engler (1908; 1913) called it. However, no supporting evidence for proposed beneficial effects due to lower chlorophyll content has yet been advanced. Thus, until any direct evidence is forthcoming, it would be more reasonable to regard the lower chlorophyll content as a side effect of physiological changes which adapt Scotch pine races to their native winter climates.

Summary

Four experiments were conducted to test the effect of intensity and quality of light, temperature, relative humidity, and daylength on the discoloration of Scotch pine. Factors were artifically altered, singly or in pairs, and the resulting needle colors were measured by comparison with Munsell Color Charts. All the factors tested had a significant effect on discoloration with the exception of relative humidity.

There appears to be a close relationship between discoloration and the physiological processes that occur when Scotch pine becomes dormant. Premature short daylengths brought about earlier discoloration, while extended daylengths prolonged green needle color into December despite freezing temperatures. Protection against freezing temperatures retarded discoloration; maintenance of temperatures above 60°F virtually eliminated discoloration.

Short photoperiods and low temperatures may effect discoloration in three ways according to current knowledge: (1) by reducing the rate of chlorophyll synthesis, (2) by exposing chlorophyll to decomposition by plant acids through the disruption of chloroplasts and protoplasm, (3) by making chlorophyll susceptible to photautoxidation due to inhibition of photosynthesis. Because the loss of green color may be reduced, or prevented altogether, by decreasing incident light intensity, or by filtering out wavelengths of light absorbed by chlorophyll, the third theory seems a plausible explanation for a major portion of the discoloration of Scotch pine.

It is suggested that rather large differences in needle color between trees growing under uniform site conditions could be explained on the basis of their differential response to photoperiod. Previous investigations have demonstrated that trees which discolor intensely tend to become dormant at an earlier date and to accumulate greater amounts of fats in their needles.

The yellow needle color of certain Scotch pine races during the winter has upon occasion been termed "protective coloration," but to this writer's knowledge no evidence favoring this viewpoint has yet been presented. Until a beneficial effect from the reduction in chlorophyll content resulting in positive genetic survival value can be demonstrated, it would be more rational to regard the yellow colora-

tion of northern Scotch pine races as merely the byproduct of physiological processes which enable the trees to survive severe winter weather.

Literature Cited

ARONOFF, S., and G. MACKINNEY. 1943. The photo-oxidation of chlorophyll. J. Amer. Chem. Soc. 65:956-958.

ASKENASY, E. 1867. Beiträge zur Kenntnis des Chlorophylls und einiger dasselbe begleitender Farbstoffe. Bot. Ztg. 25:225-230, 233-238.

BATALIN, A. 1874. Ueber die Zerstörung des Chlorophylls in den lebenden Organen. Bot. Ztg. 32:433-439.

BRAMBLE, W. C., and H. N. COPE. 1947. Races of Scotch pine and Christmas tree growing. Penna. Christmas Tree Growers' Assoc. Bull. 10:3-4.

DENUYL, D. 1956. Foliage color of pines. Ind. Christmas Tree Growers' Assoc. Bull. 5:12-15.

ECHOLS, ROBERT M. 1958. Variation in tracheid length and wood density in geographic races of Scotch pine. Yale Univ. School Forestry Bull. 64. 52 pp.

ENGLER, A. 1908. Tatsachen, Hypotesen und Irrtümer auf dem Gebiete der Samen-Provenienz Frage. Forstwiss. Centbl. 30:295-314.

———. 1913. Einfluss der Provenienz des Samens auf die Eigenschaften der forstlichen Holzgewächse. Mitt. schweiz. Central. forstl. Versuchsw. 10:189-386.

FREELAND, R. O. 1944. Apparent photosynthesis in some conifers during winter. Plant Physiol. 19(2):179-185.

GUTHRIE, J. D. 1929. Effect of environmental conditions on the chloroplast pigments. Amer. J. Bot. 16:716-746.

HABERLANDT, G. 1876a. Untersuchungen über die Winterfärbung ausdauernder Blätter. Wien. Akad. Wiss. Sitz. 72 (1):267-296.

———. 1876b. Uber den Einfluss des Frostes auf die Chlorophyllkörner. Osterr. Bot. Ztschr. 26:249-255.

HACSKAYLO, J., and W. E. GOSLIN. 1957. Forest tree physiology research at the Ohio Agricultural Experiment Station. Ohio J. Sci. 57(6):365-370.

KARSCHON, R. 1949. Untersuchungen über die physiologische Variabilität von Föhrenkeimlingen autochthoner Populationen. Mitt. schweiz. Anst. forstl. Versuchsw. 26:205-244.

KIENITZ, M. 1911. Formen und Abarten der gemeinen Kiefer (*Pinus sylvestris* L.) Ztschr. Forst-Jagdw. 43:4-35.

———. 1922. Ergebnisse der Versuchspflanzung von Kiefern verschiedener Herkunft in der Oberförsterei Chorin. Ztschr. Forst-Jagdw. 54:65-93.

KRAUS, G. 1872. Ueber die winterliche Färbung der immergrünen Gewächse. Bot. Ztg. 30:109-112, 127-128, 558-560, 588-590.

———. 1874. Winterliche Färbung grüner Pflanzentheile. Bot. Ztg. 32: 406-408.

LANGLET, O. 1936. Studier över tallens fysiologiska variabilitet och dess samband med klimatet. Medd. Stat. Skogsförsökanst. 29:219-470. (Engl. trans. in U. S. For. Ser. Translation No. 293.)

———. 1942-3. Photoperiodismus und Provenienz bei der gemeinen Kiefer (*Pinus sylvestris*). Medd. Stat. Skogsförsökanst. 33:295-327.

LARSEN, E. C. 1950. Chlorophyll formation in potato tubers as influenced by temperature and time. Science 111:206-207.

LEWIS, F. J. and G. M. TUTTLE. 1920. Osmotic properties of some plant cells at low temperatures. Ann. Bot. 34:405-416.

———. and E. M TUTTLE. 1923. On the phenomena attending seasonal changes in the organization in leaf cells of *Picea canadensis*. New Phytol. 22: 225-232.

LUBIMENKO, W. 1908. Production de la substance sèche et de la chlorophylle chez les végétaux supérieurs aux dif-

férentes intensités lumineuses. Ann. Sci. Nat. Bot. 9(7):321-415.

————, and E. R. HUBBENET. 1932. The influence of temperature on the rate of accumulation of chlorophyll in etiolated seedlings. New Phytol. 31: 26-57.

MCDERMOTT, R. E., and P. W. FLETCHER. 1955. Influence of light and nutrition on color and growth of redcedar seedlings. Mo. Agric. Expt. Sta. Bull. 587. 15 pp.

MOHL, H. 1837. Untersuchungen über die winterliche Färbung der Blätter. Flora (Ger.):673-702, 705-716.

MUNSELL COLOR CO., INC. 1952. Munsell color charts for plant tissues. 1st ed. Munsell Color Co., Inc., Baltimore, Md.

NODWELL, W. E. 1955. Some problems in selection of Scotch pine seed for better Christmas tree type. Penna. Christmas Tree Growers' Assn. Bull. 45:4-6.

PRINGSHEIM, N. 1881. Ueber Lichtwirkung und Chlorophyllfunction in der Pflanze. Jahrb. Wiss. Bot. 12:288-437.

RABINOWITCH, E. I. 1945 and 1956. Photosynthesis and related processes. Volumes I and II. Interscience Publishers, Inc., N. Y., N. Y. 2088 pp.

RUDOLPH, H. 1933. Ueber die Einwirkung des farbigen Lichtes auf die Entstehung der Chloroplastenfarbstoffe. Planta 21:104-155.

SAYRE, J. D. 1928. The development of chlorophyll in seedlings in different ranges of wavelengths of light. Plant Physiol. 3:71-77.

SCHIMPER, A. F. W. 1885. Untersuchungen über die Chlorophyllkörner und die ihnen homologen Gebilde. Jahrb. wiss. Bot. 16:1-247.

STOECKELER, J. H., and P. O. RUDOLF. 1956. Winter coloration and growth of jack pine in the nursery as affected by seed source. Ztsch. Forstgenet. 5:161-165.

STUTZMAN, L. R. 1954. The Scotch pine color problem. Penna. Christmas Tree Growers' Assn. Bull. 41: p. 3.

TUTTLE, G. M. 1919. Induced changes in reserve materials in evergreen herbaceous plants. Ann. Bot. 33:201-210.

VAARTAJA, O. 1954. Photoperiodic ecotypes of trees. Canad. J. Bot. 32:392: 399.

WAREING, P. F. 1950. Growth studies in woody species. I. Photoperiodism in first-year seedlings of *Pinus sylvestris*. II. Effect of day-length on shoot-growth in *Pinus sylvestris* after the first year. Physiol. Plant. 3(3):258-276, 300-314.

————. 1951. Growth studies in woody species. III. Further photoperiodic effects in *Pinus sylvestris*. Physiol. Plant. 4(1):41-56.

WETTSTEIN, W. von. 1954. Einfluss der Tageslänge auf das Wachstum der Kiefer (*Pinus sylvestris*). Ztschr. Forstgenet. 3: p. 142.

————. and H. GRÜLL. 1954. Das photoperiodische Verhalten von Kieferherkünften (*Pinus sylvestris* L.) Internatl. Bot. Cong. Proc. 8(13):17-19.

WIESNER, J. 1876. Die natürlichen Einrichtungen zum Schutze des Chlorophylls der lebenden Pflanze. Wien 1876. S. A. aus der Festschrift zur Feier des 25-jährigen Bestehens der K. K. Zool. bot. Gesell. Wien. p. 19-49.

ZACHAROWA, T. M. 1929. Uber den Gaswechsel der Nadelholzpflanzen im Winter. Planta 8:68-83.

Distribution of Organic Matter and Plant Nutrients in a Plantation of Scots Pine

BY
J. D. OVINGTON
H. A. I. MADGWICK

FOREST MANAGEMENT is becoming more intensive and soil fertilization is being advocated as a means of increasing forest productivity and of maintaining soil fertility. Investigations of problems of forest production and nutrition need to consider all the components of woodland communities but since forest ecosystems are variable and multi-layered structures they are difficult to sample accurately. Few data have been published showing the distribution of organic matter and nutrients within forest stands. The purpose of this account is to present such data for a plantation of Scots pine (*Pinus sylvestris* L.) and in so doing to indicate some of the difficulties encountered in sampling forest ecosystems.

Sample Plot

A rectangular plot, 20m by 25m, was marked out for sampling in a 12-acre forest compartment, at about 550 feet above sea level. The compartment forms part of the extensive coniferous plantations near the town of Jedburgh in southern Scotland. The climate is mild with an average annual temperature of about 46°F and an annual precipitation of approximately 30 inches. The soil, a heavy clay of the Hobkirk Series, is only moderately freely drained and of low base status (Muir, 1956).

Previously the area was covered with a mature woodland of Scots pine with trees 80 to 100 years old but this was clear felled in 1916. The present woodland was planted in the spring of 1924 by notch planting 2-2 seedlings of Scots pine at 3½ x 4 feet spacing. After planting, the woodland received little attention because of labor shortage so that the present stocking density has resulted mainly from the natural suppression of the less vigorous trees.

The plot contained the following living trees, 213 Scots pine, 18 birch and 1 oak, the birch and oak having established themselves naturally in the young pine plantation. In addition, there were 118 standing dead trees many of which were supported by the crowns of the surrounding trees because of the high stand density.

In October 1956 all living trees in the plot were measured for top height, bole girth at breast height and various canopy dimensions such as depth and spread of crown. The Scots pine had an average height of 49 feet and an average bole girth of 1 foot 2 inches. The sample stand would be of quality class II according to the yield tables prepared by Hummel and Christie (1953) but the lack of thinning has probably resulted in a different height and girth than might have been recorded if the plantation had been managed more actively.

The authors are, respectively, Principal Scientific and Experimental Officers of the British Nature Conservancy, Belgrave Square, London, S.W.1. At present H. A. I. Madgwick is at State University College of Forestry, Syracuse University, Syracuse, N. Y.

Methods

Sampling was restricted to pine trees since the birch and oak were relatively small and few in number. In the sample plot 207 of the 213 pine trees had boles with girths greater than 6.5 but less than 21.5 inches, i.e. within ± 7.5 inches of the average girth. The girth range was divided into five equal classes 6.5 to 9.5, 9.5 to 12.5, 12.5 to 15.5, 15.5 to 18.5 and 18.5 to 21.5 inches, the central class including trees of average girth. The girth classes are designated A, B, C, D and E respectively for simplicity of reference and their mid points are roughly equivalent to bole diameters at B.H. of 3.2, 3.7, 4.2, 4.6 and 5.0 inches.

In March 1957, the sample plot was quartered into corner quadrats and one tree of each of the five girth classes was marked for examination in each quarter, making a total of 20 trees, four of each girth class in the entire plot. The bole girth of a selected tree was always at the mid-position of the girth class it represented.

All 20 trees were felled and the roots of 17 were carefully excavated, by hand digging and winching, down to a diameter of half a centimeter. Roots with a diameter of less than half a centimeter were called rootlets and were not sampled separately for individual trees but were collected for the plot as a whole by taking eight soil cores of known volume and separating out the rootlets later. The weight of rootlets are included in the root weights given in the tables. Random circular quadrats, 81 sq cm in area, were used to sample the ground flora and litter layers, 100 quadrats per quarter for the vegetation and 15 per quarter for the litter. The sample trees, vegetation, litter and soil cores were transported quickly to the laboratory. All dry weights are given as oven dry at 80°C. For chemical analysis, samples of the plant material were ground in a Christy and Norris mill to pass through a sieve with holes having a diameter of 0.4 mm. Nitrogen was determined by the micro-Kjeldahl technique. The mineral analysis was carried out after wet digestion of the ground plant material using nitric, sulphuric and perchloric acids. The sodium and potassium contents of the resultant acid solution were determined with a flame photometer, magnesium by the titan yellow and phosphorus by the molybdate-blue method using a Spekker absorptiometer and calcium by the versenate technique.

Individual Tree Dimensions

The sample trees do not include the largest and smallest trees in the plot yet still differ greatly in size and form even though they are of identical age and originate from the same group of seedling plants. For example, some of the sample trees have a bole girth more than double that of other trees. The pines in the larger bole girth classes are taller than those of the smaller girth classes and have more elaborate and extensive root systems (Table 1). The roots of the largest tree spread about twice as far laterally and downwards as the roots of the smallest tree and similar differences occur in the spread and depth of the living crowns (Fig. 1).

The sample trees also differ considerably in dry weight, the heaviest sampled tree being twelve times as heavy as the lightest (Table 2). Trees of larger bole girth tend to be heavier in all respects having greater weights of leaves, cones, living branches, boles and roots. Bole material accounts for most of the dry weight of the trees but the relative proportions of the tree components are not constant. The percentage weight of bole material tends to decrease as tree size increases and there are corresponding increases in the percentages of crown and root material (Fig. 2). The different structures of trees of different sizes may result partly from genetical variations but can also be attributed to environmental or chance factors favoring certain trees initially so that they grow relatively rapidly during the early years to attain a more favorable position which influences tree form.

Knowing the relationship between linear dimensions and the weights of the sample

trees (Fig. 3), the weights of the remaining standing trees can be estimated from their height and bole girth measurements. Since tree height is sometimes difficult to measure accurately in dense woodlands and proved to be fairly closely correlated with bole girth, regression equations have been calculated relating tree weight to bole girth only (Table 3). Although some variation occurs between trees of the same girth class, the weights of the various tree parts are closely correlated with bole girth but the regression equations differ for different tree parts. In determining the total dry weight of individual trees, it is advisable to consider each component separately in order to avoid errors caused by the changing proportions of leaf, branch, bole and root material as the bole size increases. The weight of cones per tree is small and variable so that it has not been included in the estimates of tree weight and nutrient content.

Nutrient Content of the Trees

The concentrations of various plant nutrients in the leaves, branches, bole and roots of the sample trees were determined and the averages for each girth class are shown in Figure 4. The percentages of the nutrients decrease consistently in the order: leaves, living branches, roots and boles except that the percentage of calcium in the boles is larger than that of the roots. In most cases, the nutrient concentration also decreases as tree size increases so that 20 of the 23 linear correlations between tree girth and nutrient concentration are negative, ten significantly so (Table 4). Wright

TABLE 1. Dimensions of sample trees.

Tree number	Girth class[1]	Height	Number of whorls with living branches	Number of primary living branches	Total length of primary living branches	Number of main lateral roots	Length of longest root (over 0.5cm diameter)	Maximum root depth in soil
		m			*m*		*m*	*m*
1	A	8.9	11	28	13.6	2	0.7	0.4
2	A	10.4	12	28	15.3	5	0.8	0.4
3	A	9.3	10	27	11.7	3	0.7	0.5
4	A	9.5	12	33	18.8	7	0.9	0.5
5	B	10.1	10	30	20.1	Roots not sampled		
6	B	11.5	11	47	32.0	3	1.0	0.6
7	B	11.8	11	42	29.3	4	0.9	0.6
8	B	11.6	12	50	34.2	5	0.9	0.5
9	C	12.1	13	69	54.1	6	1.0	0.6
10	C	12.3	11	51	39.7	6	1.6	0.7
11	C	12.7	13	44	42.3	7	1.5	0.6
12	C	12.3	13	51	43.8	5	0.8	0.7
13	D	12.2	13	62	40.0	6	0.9	0.6
14	D	12.3	13	48	49.3	5	1.2	0.7
15	D	12.5	12	51	49.6	5	1.7	0.4
16	D	12.2	11	58	51.1	5	....	0.8
17	E	13.0	10	52	54.2	Roots not sampled		
18	E	12.6	16	83	89.6	Roots not sampled		
19	E	13.3	13	70	78.3	7	1.8	0.8
20	E	14.0	16	56	79.2	7	1.1	0.7

[1]Each girth class in terms of d.b.h. in inches is approximately as follows: A = 3.2; B = 3.7; C = 4.2; D = 4.6; and E = 5.0.

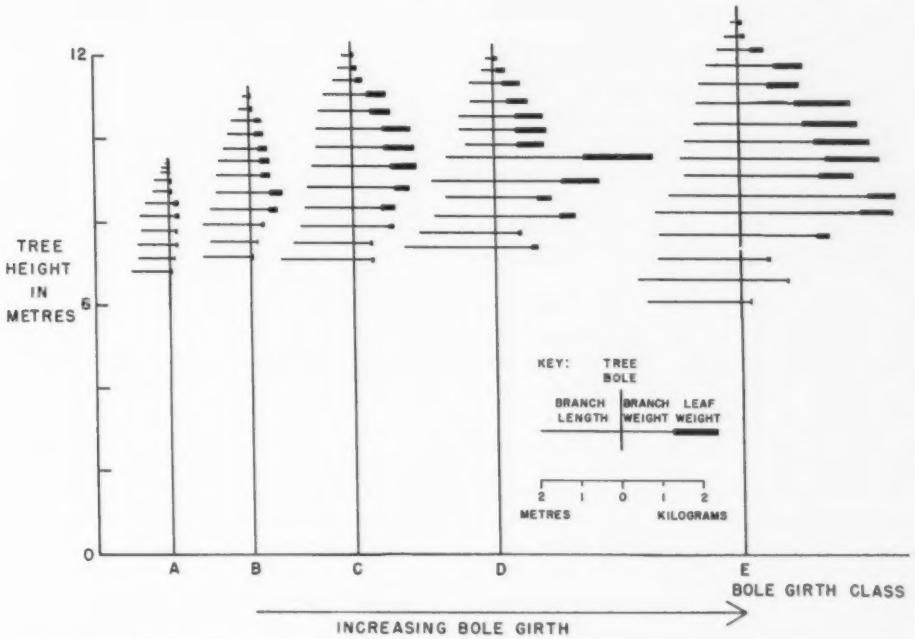


FIGURE 1. *The average whorl heights, branch length and fresh weights of branches and leaves for trees of different girth classes.*

TABLE 2. Oven-dry weights (Kg) of sample trees.

Tree number	Girth class	Leaves	Living branches	Cones	Bole	Living shoot	Dead branches	Roots
1	A	0.1	0.3	0	6.1	6.5	1.1	0.9
2	A	0.1	0.3	0	7.4	7.8	0.8	1.8
3	A	0.1	0.2	0	7.5	7.8	0.8	2.1
4	A	0.2	0.5	0	7.6	8.3	0.4	1.6
5	B	0.3	0.9	0	13.5	14.7	2.0	Not collected
6	B	0.8	1.1	0	15.2	17.1	0.4	3.3
7	B	0.8	1.1	0.01	16.2	18.1	0.9	3.5
8	B	0.6	1.3	0	16.8	18.7	1.6	4.5
9	C	1.3	3.0	0	24.1	28.4	2.0	6.6
10	C	1.5	2.4	0.01	27.9	31.8	1.5	6.9
11	C	1.8	4.0	0.02	28.9	34.7	3.1	7.0
12	C	1.9	2.4	0	30.7	35.0	1.4	7.0
13	D	2.6	2.9	0.04	34.5	40.0	2.2	7.3
14	D	2.9	5.5	0	38.0	46.4	2.8	12.7
15	D	2.7	4.7	0	40.7	48.1	5.0	13.5
16	D	3.0	5.1	0.04	41.5	49.6	4.3	8.1
17	E	2.9	4.9	0.02	52.6	60.4	3.6	Not collected
18	E	3.8	9.4	0.10	50.2	63.5	4.6	Not collected
19	E	4.6	10.0	0.01	56.5	71.1	5.8	19.2
20	E	4.4	11.8	0	64.0	80.2	4.0	18.1

and Will (1958) and Ovington and Madgwick (1959) have obtained similar results for pine and birch respectively but Leyton and Armson (1955) have recorded positive correlations between tree growth and foliar concentrations of nitrogen, phosphorus and potassium. Leyton and Armson sampled needles only from the uppermost whorls of Scots pine so that their results of foliar analysis are probably not representative of the whole leaf mass.

By combining the dry weight and percentage chemical composition data, the total weight of plant nutrients in the sample trees can be calculated and the averages for trees of each girth class are given in Table 5. The percentages of sodium in some bole samples were too small to be measured accurately by the analytical techniques used so that the weights of sodium in the tree boles are not given. The different concentrations of nutrients in leaves, branches, boles or roots result in a different weight distribution of nutrients as compared with dry matter within the trees. For example, leaf material represents 2 to 5 percent of the dry weight of the trees but contains 8 to 36 percent of the weight of nutrients. In contrast the tree boles usually constitute about three quarters of the total dry weight but contain less than half of the

TABLE 3. Regression equations for tree weights and bole girths.

Tree part		Standard error
Leaves	$\log_{10}W = 3.63 \log_{10}g - 2.57$	0.11
Living branches	$\log_{10}W = 3.52 \log_{10}g - 2.21$	0.12
Dead branches	$\log_{10}W = 2.08 \log_{10}g - 1.23$	0.18
Boles	$\log_{10}W = 2.23 \log_{10}g - 0.24$	0.04
Roots	$\log_{10}W = 2.60 \log_{10}g - 1.11$	0.10
Living tree (exclusive of rootlets)	$\log_{10}W = 2.47 \log_{10}g - 0.25$	0.05

W = oven dry weight (Kg).
g = bole girth at breast height (cm).

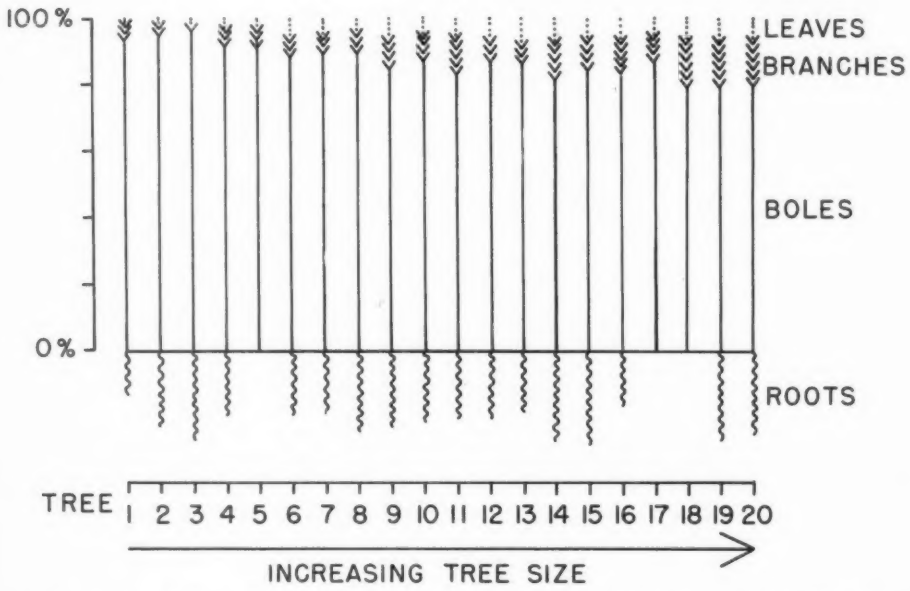


FIGURE 2. *The relative proportions of sample trees as percentages of the oven dry weight of the living shoot.*

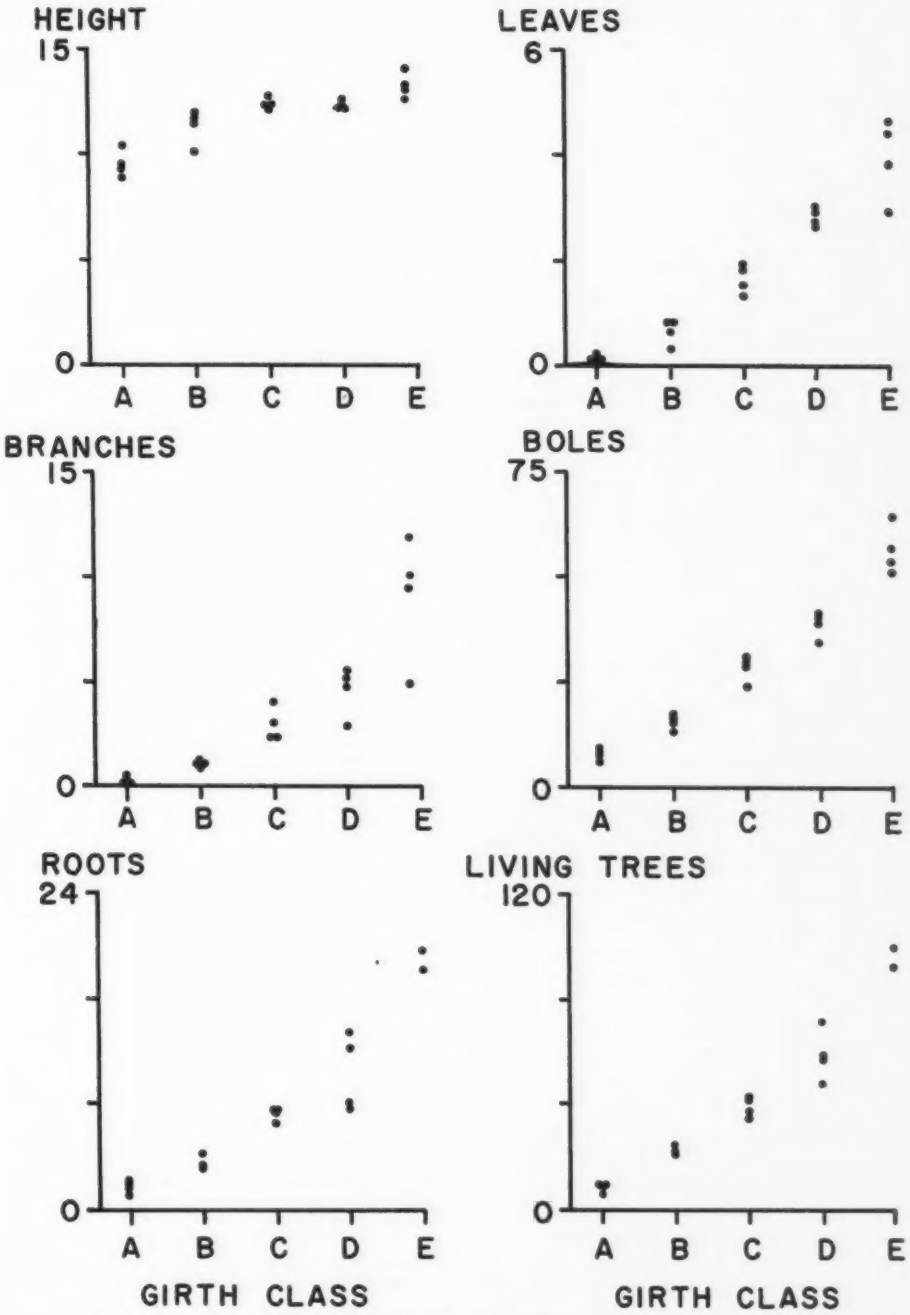


FIGURE 3. *The relationship between tree height (m), dry weight (Kg) of tree parts and bole girth class.*

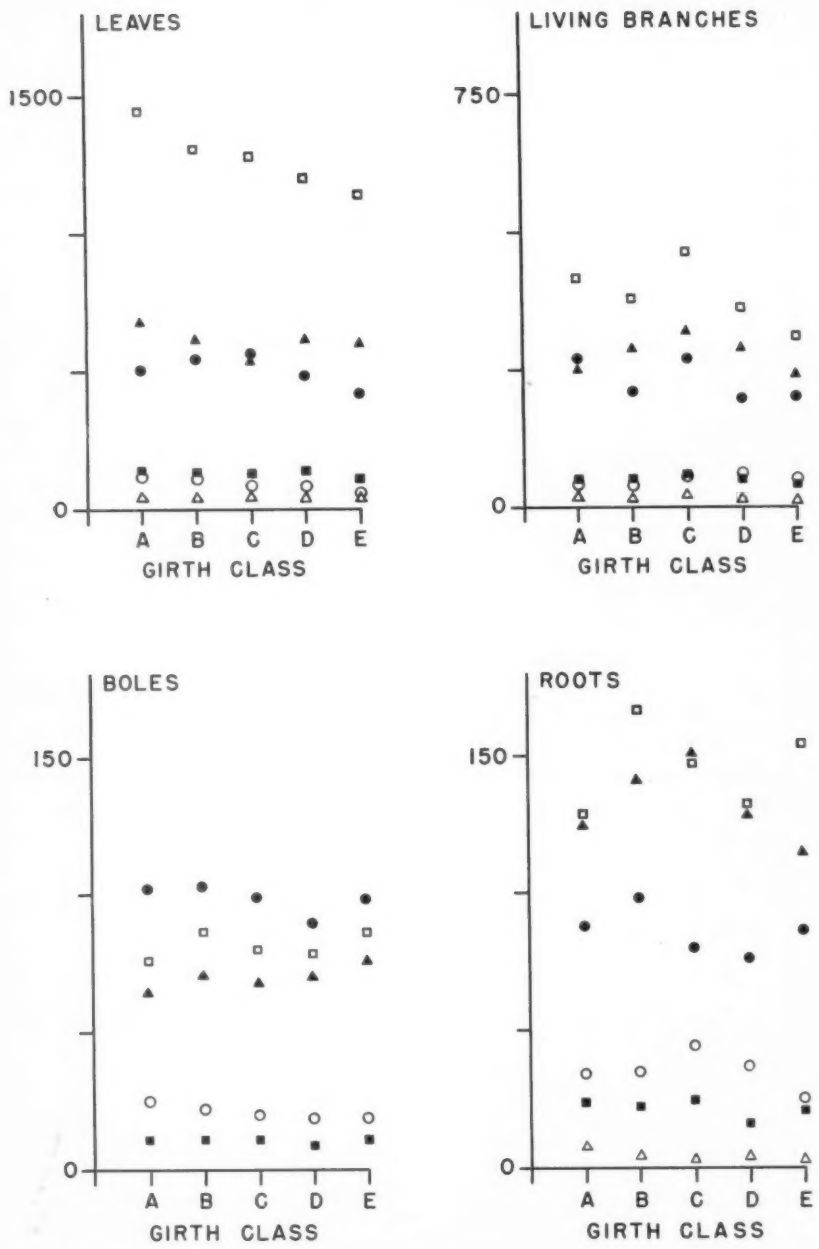


FIGURE 4. *The average nutrient concentration (mg/100g O.D.) of tree parts.*

TABLE 4. Correlation coefficients between nutrient concentration and bole girth.

	Leaves	Living branches	Boles	Roots
Sodium	−0.029	−0.377	....	−0.612**
Potassium	−0.263	−0.039	+0.387	−0.075
Calcium	−0.484*	−0.434*	−0.258	−0.319
Magnesium	−0.863***	−0.440*	−0.821***	−0.081
Phosphorus	−0.457*	−0.465*	−0.102	−0.409
Nitrogen	−0.663**	−0.442*	+0.211	+0.114

*Significant at the 5% level.
**Significant at the 1% level.
***Significant at the 0.1% level.

nutrients in the trees.

Although the percentages of nutrients in the smaller trees are greater than those in the larger trees, the differences in dry weight are so great that the larger trees contain a greater weight of plant nutrients. However, differences in nutrient content are not so marked as differences in dry weight, for instance the trees of the largest girth class carry over 30 times the weight of leaves on trees of the smallest girth class but their leaves contain only 10 to 25 times the amount of nutrients.

Weight and Nutrient Content of Tree Stock

The total dry weight and the nutrient content of all the pine trees in the stand can be estimated using three principal techniques. (1) Trees of average bole girth may be assumed to be of average dry weight and chemical composition so that the weights for the tree stock can be estimated by multiplying the average data by the number of trees in the stand. (2) Trees of average bole girth may be assumed to be of average dry weight and chemical composition for the girth class they represent. The totals for each class can be calculated by multiplying the average data by the relevant number of trees in each girth class. The plantation weights are determined by summing the results for each girth class. Unusually small or large trees outside the measured girth class range are included in the smallest and largest girth classes respectively. (3) The formula given in Table 3 can be used to calculate the weight and nutrient content of each tree from its bole girth. The weight of the tree stock is obtained by adding the individual tree data.

The dry weight of the tree stock has been calculated using all three methods and the results are given in Table 6. Comparisons of the three sets of dry weight data on an area basis show that method (1) gives consistently low results compared with methods (2) and (3), whilst method (2) tends to give slightly smaller values than method (3). Method (1) is undoubtedly the most unreliable of the three, for it is clear from the individual tree data that trees of average bole girth are not average in other respects so that a serious underestimate of the weight of the tree stock results. In fact a truly "average" tree does not exist in the stand since a tree of average bole weight would have a different bole girth to that of a tree carrying the average weight of leaves. The smaller values, particularly of bole weights, obtained by method (2) compared with those of method (3) are in part due to the sample trees not being representative of their girth class but are also due to the failure to account adequately for the few but relatively large trees occurring outside the sampled girth range. In the sample plot there were five trees having

TABLE 5. The average nutrient content (g) of sampled trees in different girth classes.

	Girth class				
	A	B	C	D	E
Number of trees	28 + 1	50	65	41	23 + 5
Sodium					
Leaves	0.07	0.23	0.67	1.01	1.72
Living branches	0.07	0.17	0.59	0.62	1.19
Dead branches	0.09	0.16	0.34	0.46	0.75
Bole	Too small to be determined by analytical techniques				
Roots	0.12	0.13	0.23	0.37	0.58
Potassium					
Leaves	1.0	3.8	8.5	17.1	23.6
Living branches	0.9	3.2	9.7	13.0	20.9
Dead branches	0.2	0.5	0.6	1.4	1.8
Bole	4.7	11.0	18.6	27.0	42.2
Roots	2.0	5.3	10.3	13.1	21.5
Calcium					
Leaves	0.8	3.5	9.1	13.6	16.4
Living branches	0.9	2.4	7.9	8.8	18.0
Dead branches	0.9	1.5	3.1	5.1	5.8
Bole	7.3	16.2	27.5	34.8	54.6
Roots	1.4	3.8	5.5	7.9	16.1
Magnesium					
Leaves	0.2	0.7	1.4	2.2	2.2
Living branches	0.1	0.4	1.7	2.7	4.4
Dead branches	0.1	0.2	0.4	0.8	1.0
Bole	1.8	3.3	5.6	7.4	10.5
Roots	0.5	1.4	3.0	3.6	4.6
Phosphorus					
Leaves	0.2	0.8	2.0	3.8	4.3
Living branches	0.2	0.6	2.2	2.1	3.4
Dead branches	0.2	0.2	0.4	0.6	0.8
Bole	0.8	1.7	3.0	3.6	6.2
Roots	0.4	0.8	1.6	1.7	3.9
Nitrogen					
Leaves	2.2	8.2	20.5	33.4	45.2
Living branches	1.4	4.3	13.9	16.5	27.5
Dead branches	2.3	3.3	5.6	9.4	13.7
Bole	5.5	13.4	22.5	29.7	47.6
Roots	2.1	6.3	10.1	13.5	28.8

a bole girth greater than the sampled range and only one tree with a bole girth smaller than the lowest value of the sample range.

Differences in the nutrient content of the tree stock estimated by the three methods reflect the dry weight differences, thus method (1) gives consistently low results but there is a general agreement between

methods (2) and (3).

Distribution of Organic Matter and Nutrients

The weights of organic matter and of nutrients in the tree stock (calculated by method (2)) and in other components of the plantation are given in Table 7. The ground flora, mainly of wood sorrell *Oxalis acetosella*, was very sparse and plants were present in only 21 of the 400 quadrats. The estimate of rootlet weight is probably subject to considerable error since only eight soil cores were collected and sampling was restricted to the top 12.5 cm of soil, where the rootlets appeared to be most abundant.

Thirty-three years after planting, most of the organic matter in the plantation has been produced by the trees and is divided almost equally between living trees and dead material i.e. litter and dead trees. On average, organic matter has accumulated at the rate of 9,276 kg per hectare per annum. The current rate of accumulation is probably greater than this since the average value for the 33 years would be reduced by including the early period of low productivity when a closed forest cover had not developed (Ovington 1957, 1959).

TABLE 6. The total oven dry weight (Kg/ha) of all trees by parts in the plot, calculated by three different methods (See text for explanation of methods).

Tree part	Method 1	2	3
Leaves	0.34	0.37	0.38
Living branches	0.63	0.70	0.72
Dead branches	0.43	0.49	0.47
Boles	5.94	5.94	6.03
Roots	1.47	1.63	1.64
Living trees	8.39	8.89	9.02

The surface humus layer completely covers the mineral soil and is composed almost entirely of decomposing tree leaves and branches. The thickness of this layer varies greatly but it is about 12 cm thick giving a weight of 111,000 kg per hectare

TABLE 7. Distribution of organic matter and nutrients in the 33-year-old plantation of Pinus sylvestris *(Kg/ha).*

Item	O.D. weight	Sodium	Potassium	Calcium	Magnesium	Phosphorus	Nitrogen
Leaves	7300	3	43	36	6	9	89
Living branches	14000	2	39	30	7	7	52
Dead branches	9700	1	4	13	2	2	27
Boles	118800	—	84	115	24	12	97
Roots	32700	1	43	27	11	7	48
Rootlets	3400	1	11	6	2	4	33
Total for living trees	185900	8	224	227	52	41	346
Ground flora	10	<1	<1	<1	<1	<1	<1
Dead trees (exclusive of root system)	9600	1	1	6	<1	<1	9
Fresh litter (L)	2900	1	3	11	1	2	28
More decomposed litter (F + H)	107700	33	162	311	30	76	1594
Total	306100	43	390	555	83	119	1977

(standard deviation 29,600). The initial breakdown of the litter falling from the trees must be fairly rapid since the weight of fresh litter is equivalent to about a year's leaf fall. Compared with other woodlands (Ehwald 1957), the lowermost layer of more highly decomposed litter has tended to accumulate in excessive amounts probably as a result of the lack of thinning. The litter and dead trees contain a significant proportion of the total nutrients in the organic matter of the forest ecosystem, about 42 percent of the potassium, 59 percent of the calcium, 39 percent of the magnesium, 66 percent of the phosphorus and 82 percent of the nitrogen. If the litter were removed there would be a serious drain on the nutrient capital and conversely if litter breakdown was stimulated large amounts of plant nutrients would become available to the trees.

Tree leaves, branches and small rootlets tend to be short lived compared with the boles and roots which account for over 80 percent of the total dry weight of the living stock. If all the living tree boles were harvested, large amounts of plant nutrients would be removed amounting to about 22 percent of the potassium, 21 percent of the calcium, 29 percent of the magnesium, 10 percent of the phosphorus and 5 percent of the nitrogen contained in the organic matter of the plot.

Conclusions

Compared with agricultural, horticultural and aquatic crops, relatively little is known of the distribution and circulation of organic matter and plant nutrients in forest communities. Such information would be valuable in assessing the importance of site factors in controlling forest productivity and can also be applied to other problems for example, of forest site classification or of evaluating the gross role of the associated flora and fauna in the community dynamics. Inevitably, the sampling of forest ecosystems entails a considerable expenditure of effort so that it is important to develop sampling techniques which will give reasonably accurate results for the minimum expenditure of time.

The problem of determining the dry weight and nutrient content of a tree stand is complicated because of the diversity of tree size, the different proportions of leaf, branch, bole and root material in trees of different size and the different concentrations of nutrients in the tree components. The most accurate sampling method would be to sample a large number of trees covering the size range present in the stand and to determine regression equations relating dry weight and nutrient content to certain linear dimensions. This method is inevitably laborious, since all the trees in the stand have to be considered separately in arriving at the total weight of the stand. The technique of using sample trees for a range of size classes is not so accurate as the previous method but has the advantage of being relatively rapid. In some instances for example in sampling long-term experimental plots of small size, the number of trees that can be examined may be severely limited so that it is important to select the sample tree or trees carefully for both bole and canopy characteristics. The results obtained by this method can only be very approximate and the accuracy depends upon the uniformity of trees within the stand.

The paucity of the ground flora is unusual for a plantation of Scots pine at this age in Britain and reflects the density and dominance of the tree cover. Most of the organic matter in the stand has been produced by the trees and the build up of organic matter has immobilized significant amounts of plant nutrients, about 1 kilogram of sodium, 12 of potassium, 17 of calcium, 3 of magnesium, 4 of phosphorus and 60 of nitrogen per hectare per annum. The annual production of organic matter and uptake of plant nutrients must have been greatly in excess of these values for some decomposition of litter will have taken place.

Summary

1. The dry weights and nutrient contents are given for 20 sample trees of different sizes in a plantation of Scots pine.

2. The dry weight of the tree stock is calculated by three methods.
3. The dry weight and nutrient content of the tree stock, the dead trees, the ground flora and the humus layer in the sample plot are tabulated.

Literature Cited

EHWALD, E. 1957. Uber den Nährstoffkreislauf des Waldes. S. B. Dtsch. Akad. Landw. Berlin. 4: 1-56.

HUMMEL, F. C. and J. CHRISTIE. 1953. Revised yield tables for conifers in Great Britain. For. Comm. For. Rec. No. 24: 23 pp.

LEYTON, L. and K. A. ARMSON. 1955. Mineral composition of the foliage in relation to the growth of Scots pine. For. Sci. 1: 210-218.

MUIR, J. W. 1956. The soils around Jedburgh and Morebattle. Memoirs of the Soil Survey of Great Britain.

OVINGTON, J. D. 1957. Dry-matter production by *Pinus sylvestris* L. Ann. Bot. N.S. 21: 287-314.

OVINGTON, J. D. 1959. Mineral content of plantations of *Pinus sylvestris* L. Ann. Bot. N.S. 23: 75-88.

OVINGTON, J. D. and H. A. I. MADGWICK. 1959. The growth and composition of natural stands of birch. 2. The uptake of mineral nutrients. Plant and Soil. 10: 389-400.

WRIGHT, T. W. and G. M. WILL. 1958. The nutrient content of Scots and Corsican pines growing on sand dunes. Forestry. 31: 13-25.

Economics of American Forestry

By Albert C. Worrell. John Wiley & Sons, Inc., New York. 441 pp., illus. 1959. $9.75

Review by C. H. Stoltenberg
Northeastern Forest Experiment Station, U. S. Forest Service.

Professors teaching undergraduate courses in the economics of forestry will welcome enthusiastically this much needed treatise. It is primarily a textbook intended for the undergraduate forestry student and most useful to one who knows something about forestry but very little about economics.

Using a multitude of practical examples from almost every phase of forestry activity, Professor Worrell has tried to help the student understand the many economic relationships that exist in forestry. I believe instructors in forestry economics will find that he has succeeded admirably.

Using the terminology of economics, the books provides a theoretical explanation of such economic relationships in forestry as why people own forest land, why they manage it as they do, why others buy forest products, why they operate their sawmills and wood procurement facilities as they do, why one product is manufactured rather than another, and how product prices are determined and what makes them change. It also suggests ways economic analysis can contribute to a more efficient use of land, manpower, and capital in forestry activities.

This book should also help students see forestry in a broader social frame of reference. It should help them understand how silviculture, protection, management, utilization, and other specialties all contribute knowledge that enables people to use forest resources so that they will provide the things that people want most from them.

But the very breadth of the book's subject matter necessarily limits the depth of treatment that can be given to any single subject. It introduces the reader to production economics, marketing, valuation, consumption, price theory, and land economics, but it probably will not provide an actual working knowledge of the tools and subject matter of any of these areas. For this reason, the usefulness of the book to practicing foresters is somewhat limited. Research foresters who have not had special training in economics may find it useful as an outline of the major principles that apply to various forestry problems. But it clearly is not a how-to-do-it manual of economic analysis.

Brooming Response of Black Spruce to Dwarfmistletoe Infection

BY
RALPH L. ANDERSON
F. H. KAUFERT

THE PARASITIC PLANT dwarfmistletoe (*Arceuthobium pusillum* Peck) causes witches'-broom and is one of the most serious diseases of black spruce (*Picea mariana* (Mill.) B.S.P.). It infects trees of all ages and all crown and vigor classes from rapidly growing dominants to severely suppressed trees.

The genus *Arceuthobium* has been monographed by Gill (1935), and a more recent review of literature has been made by Kuijt (1955). In a previous paper Anderson and Kaufert (1953) described the occurrence of dwarfmistletoe on black spruce and the damage caused, and suggested control measures.

During this study of dwarfmistletoe damage to black spruce in northern Minnesota, marked variations in the reaction of the host to infection were noted. The purpose of this paper is to describe these variations and suggest the reasons for them. Heinricher (1918) has presented a good discussion of witches'-broom development for a European dwarfmistletoe, but little has been published on American species.

The information presented here is based on two general types of field study. In 1947, 31 infected areas ranging from 1 to 640 acres in size were given a detailed examination. This was an exploratory study with the primary objective of relating the characteristics of infection and damage caused to such factors as site characteristics, stand age, stand density, and stand structure. In 1948, 12 permanent study plots were established, where detailed measurement and classification data were collected on 273 infected trees and 728 witches'-brooms. All of the permanent plots and most of the infected areas studied in 1947 are located in the extensive black spruce swamp stands of Koochiching County, Minn. The remainder of the areas studied in 1947 are on swamp sites in Aitkin, Carlton, Itasca, and Lake Counties.

Variations in Witches'-Broom Development

By far the most apparent and commonly observed reaction of the host to dwarfmistletoe infection is the abnormal and excessive growth of infected branches, re-

---

The authors are respectively Plant Pathologist, Lake States Forest Experiment Station, maintained at St. Paul, Minn., by the Forest Service, U. S. Depart. Agric., in cooperation with the University of Minnesota; and Director, School of Forestry, University of Minnesota.

The study was conducted in 1947-48 on Minnesota and Ontario Paper Company Graduate Research Fellowships while the senior author was a graduate student in the Minnesota School of Forestry. Appreciation is expressed to the Minnesota and Ontario Paper Company for making the study possible and to foresters of the same company, of Halvorson Trees, Inc., and of the Division of Forestry, Minnesota Conservation Department, for advice and field assistance. Published as Minn. Agric. Expt. Sta. Sci. Jour. Series Paper No. 3908.

ferred to as witches'-brooms. The basic physiological reactions involved in this stimulation are not definitely known.

Some of the witches'-brooms contained a few twigs and branches that bore no dwarfmistletoe shoots or evidence of having had shoots in previous years.[1] These twigs and branches did, however, have the growth pattern that is associated with dwarfmistletoe infection. It is not known for certain whether these twigs were stimulated by the nearby infection in other branches on the broom or whether the cortical system of the dwarfmistletoe was present without forming shoots.

A knowledge of the frequency of witches'-broom-free infection (that is, dwarfmistletoe infection that does not stimulate the tree to form a broom) is vital for the application of control measures requiring eradication of infected materials. Such infections, of course, can be detected only by close examination of twigs and branches for the presence of the small dwarfmistletoe shoots. To determine the occurrence of broom-free infections, examinations were made of all branches on several hundred trees in heavily infected areas. Only five broom-free infections were found.

These five witches'-broom-free infections were on old trees and on long, low branches that received very little if any direct light. The branches were apparently normal for this low light intensity except for the presence of dwarfmistletoe shoots on the usual interwhorls.[2] The shoot vigor was poor and seed production by the parasite very low. In view of their low frequency and poor vigor, broom-free infections probably are not of great consequence.

Dwarfmistletoe infection causes three types of symptom expression in that the characteristics of the witches'-brooms formed vary with the vigor of the host. There are two principal broom types. The name "bush-type" was selected for those typical of low-vigor hosts and "leader-type" for those typical of high-vigor hosts. Most brooms definitely fall in one of these classes, but a few do not. These exceptions occur on long, weak-looking branches which receive very little light and, in fact, are formed under conditions similar to those where broom-free infections were found. This minor broom development is designated as the "weak-type."

Von Schrenk (1900), who studied dwarfmistletoe on black spruce in Maine, stated that witches'-brooms are of two forms, but he apparently classified them according to vigor of the infected branch rather than the overall vigor of the host. Both the bush-type and leader-type described above belong to the group he described as growing on vigorous branches. Most of the brooms difficult to classify as either leader- or bush-type fit Von Schrenk's description of brooms formed on weak branches.

The bush-type witches'-broom forms when infection occurs on older trees or on young trees of low vigor. This type of broom is apparently a result of the host's relatively low capacity for growth.[3] Such a broom consists of a dense mass of slender branchlets radiating from the area on the branch where the infection originated. These branchlets turn more or less upward and are approximately the same length (Fig. 1).

Most old bush-type witches'-brooms are 2 to 5 feet in diameter, but an occasional broom may be as much as 10 feet across.

[1]On black spruce the basal part of shoots persists in the bark for several years.

[2]Mature shoots are on 3-year-old growth and immature shoots on 2-year-old growth—never on younger growth and very rarely on 4-year-old growth.

[3]Low capacity for growth as used here refers to the fact that because of age or unfavorable environment, such trees even when healthy, grow slowly and therefore have a limited response to the stimulation caused by dwarfmistletoe.

The diameter of the branch bearing the broom increases considerably, and the branch tends to arch upward. Sometimes, especially when the infection is far out on a long branch, this thickening is not well developed and may be limited to the vicinity of the broom; then the branch hangs downward. Infrequently, even though the branch may have thickened somewhat clear to the trunk, it is not strong enough to support the weight of the broom. Then the branch supporting the broom may break or the broom, which originally grew erect, will "capsize"—that is, twist to a downward position. When this happens, the broom branchlets may continue to grow, again turning upward.

The leader-type witches'-broom is formed when young, vigorously growing trees are infected. The name leader-type does not indicate that such brooms develop only on the leaders of infected trees; rather, it is descriptive of the growth pattern of brooms that develop regardless of the position of the infection on the tree. The broom has a leader in the same sense that a coniferous tree does. Tables 1 and 2 show the predominance of this type of broom on the smaller trees. The data are from random samples in an all-aged, relatively open-grown stand. They reflect the fact that leader-type brooms develop on the younger and more rapidly growing trees. Either the tip of the infected branch or a branchlet becomes in effect a fast-growing leader (Fig. 2). Most of the growth acceleration is expressed by the broom leader rather than being more or less equally distributed among the broom's

FIGURE 1. *A black spruce with a large, old bush-type dwarfmistletoe witches'-broom, indicating an advanced stage of infection. Notice the sparse foliage of the crown above the broom.*

TABLE 1. Distribution of witches'-brooms[1] as related to tree height.

Tree d.b.h. class (inches)	Number of witches'-brooms			Leader-type brooms as a percent of total
	Leader-type	Bush type	Total	
1–2	61	17	78	78
3–4	31	30	61	51
5–6	8	28	36	22
7–8	4	13	17	24

[1]Young, vigorous brooms only. Old brooms are not included.

TABLE 2. Distribution of witches'-brooms[1] as related to tree height.

Tree height class (feet)	Number of witches'-brooms			Leader-type brooms as a percent of total
	Leader-type	Bush-type	Total	
10	63	20	83	76
20	28	20	48	58
30	30	32	62	48
40	18	37	55	33
50	2	8	10	20

[1]Young, vigorous brooms only. Old brooms are not included.

branchlets as in the bush-type broom. The leader-type broom thus acquires a form similar to the parent tree except that its branches are usually more slender and finely divided. This infected branch continues to grow upward and increases in diameter very rapidly, often ultimately exceeding the diameter of the bole of the tree above its union with the infected branch (Fig. 3).

The literature contains little comment on this type of witches'-broom development. Pomerleau (1942) mentions that the broomed branch often grows as vigorously as the trunk and so causes the formation of a double trunk. Freeman (1905) mentions that there is a lateral leader effect, and Dowding (1929) states that there is a strong negative geotropic effect. Himmel (1935) gives a good description of the leader-type response to what he suspected was dwarfmistletoe infection on black spruce. His description and illustration leave little doubt that dwarfmistletoe was the cause. The looping he describes as occurring before the broom develops an upright growth has been noted by the authors on dwarfmistletoe infections but is rather uncommon.

FIGURE 2. *A young leader-type witches'-broom on black spruce. The infected branch has turned upward and is growing rapidly.*

FIGURE 3. *A black spruce with large, old leader-type witches'-brooms. The deformation is more severe than that caused by bush-type brooms* (*Fig. 1*).

The leader-type witches'-brooms affect the growth of the host tree much more than do the bush-type brooms. The extent of deformation is much greater. During the period of vigorous broom growth the diameter growth of the bole below the infected branch is greatly increased. Eventually both tree diameter growth and broom growth drop off rapidly and markedly. Furthermore, since such leader-type brooms

normally form on young trees, most of them originate on branches below a height of about 9 feet. The temporary acceleration of growth is limited to a very small part of the bole. For the part of the tree above the infected branch, a decided drop in increment occurs as soon as the broom starts to develop. Infections that produce either leader-type or bush-type brooms can cause mortality. Since the bush-type broom usually forms on the older merchantable-size trees, they can be salvaged. The serious growth reduction and deformation caused by leader-type brooms on younger trees usually preclude any salvage value.

Height growth is materially affected by dwarfmistletoe infections that induce leader-type witches'-brooms. In a number of sapling stands healthy trees were found to be growing about 8 inches in height per year, but on trees of the same age with leader-type brooms the growth of the true leader was usually reduced to 1 to 3 inches. In contrast, the broom leaders were sometimes making as much as 12 to 18 inches height growth and, in most cases, growing at about the same rate as the true leader on noninfected trees. On many trees the broom ultimately exceeds the height of the tree by several feet, and the broom may reach a total length of as much as 20 feet. These observations of intermingled clean and infected trees of the same age show clearly that this type of infection causes a marked reduction in the height growth of affected trees.

Leader-type infections on seedlings and small saplings result in serious damage and mortality. Some small trees appeared to be heavily infected but free of witches'-broom-ing. Careful examination proved that this was not true. What appeared to be the "tree" was invariably just a leader-type broom, the original stem having disappeared. Infection had occurred on a branch very close to the ground and sphagnum moss had grown over the junction of the infected branch and remaining stub of the original trunk (Fig. 4). Other small trees had become infected on a higher branch, and the original stem above this point had died. The point of infection in a few small trees apparently had been on the leader, since the tree was topped by a broom, with no evidence that there had been an older leader, later suppressed by a broom originating on a lateral branch.

The extreme reaction to a single infection, in which the witches'-broom suppresses the main stem, appears to be largely limited to seedlings and small saplings. "Trees" that consist only of a leader-type witches'-broom could easily be mistaken for trees with systemic infection. No true systemic infection was found. In every case it was evident that the infection had spread only toward the growing tips of the branches from the original point of infection and not back toward or down the stem existing at the time of infection. Although these "trees" usually die by the time they are about 4 to 6 feet high, occasional larger specimens are found.

Phases of Witches'-Broom Development

One of the first symptoms of infection on a branch is a fusiform swelling about a foot long centered at the point of infection. This swelling is neither so conspicuous nor so well developed as some other dwarfmistletoe species (Weir 1916). Witches'-broom development begins as a result of stimulation of the branchlets on this swollen area. New infections can be detected by the swollen area and lush growth of the branchlets. During the early stages of infection the rapid growth of the fusiform swelling, of the basal parts of the broom, and of the stem of the branch bearing the broom results in abnormal bark formation. Normal scaly bark formation does not appear to keep up with growth. Hence the bark in such areas tends to be orange colored, resembling that of young Scotch pine (*Pinus sylvestris* L.) branches. The broom usually grows rapidly for only 5 to 10 years. During this time the broom foliage is very luxuriant. The needles are dark green, long, numerous, and appear superior to those found on healthy trees. This abnor-

mal foliage has also been noted by Weir (1916) on western conifers.

During the stimulated growth period dwarfmistletoe shoots are also numerous and vigorous, and seed production by the parasite appears to be much greater than in later life. Some of the nutrients produced by the entire tree apparently are diverted to the infected parts, as has been mentioned by other investigators (Hedgcock 1915, Weir 1918).

The growth rate and vigor of the witches'-broom decline quite abruptly, and the foliage on the broom becomes successively thinner. The newer needles are smaller and light yellowish-green, indicating a reduction in chlorophyll content. The abnormality in color is so great that old brooms can be detected against a background of normal foliage at a greater distance than the broom can be detected by its form. This loss of vigor is well described for western species (Korstian and Long 1922, Weir 1916). Dowding (1929), who studied *Arceuthobium americanum* Nutt. ex. Engelm., states that reduction in foliage occurs only on female infections. This was not found to be true for *A. pusillum*.

The above analysis of growth and vigor as related to age of infections was based on data obtained by boring the infected branches and counting the annual rings outward from the point where rapid growth started.

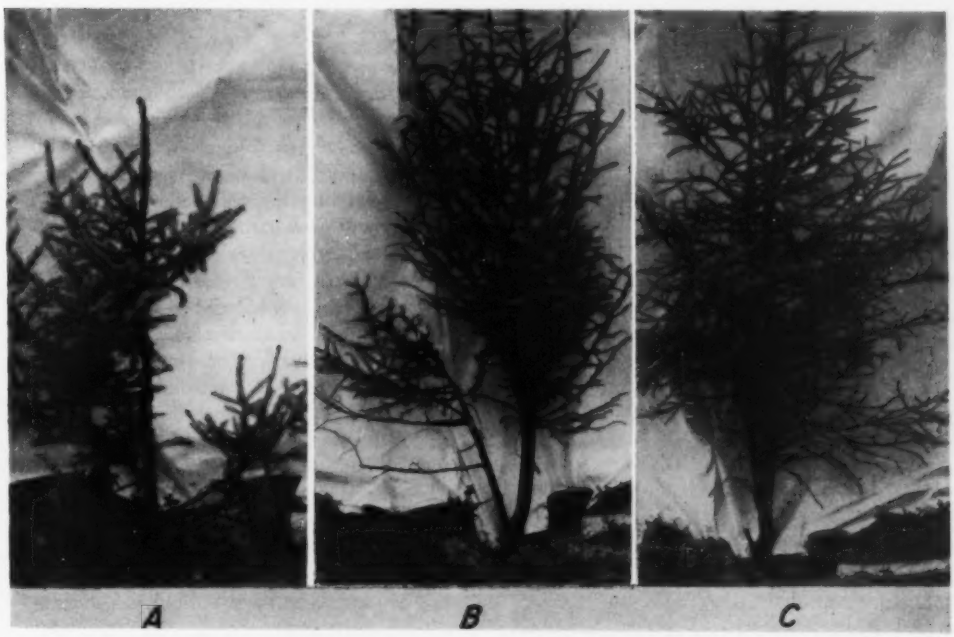


FIGURE 4. *A. Young dwarfmistletoe witches'-broom starting to develop on low branch to right of tree stem. B. A later stage of broom development. The broom at right has grown much faster than the original tree at left, which is being "suppressed." C. Final stage of broom development from an infection similar to those in A and B. Original stem has disappeared except for small dead stub persisting on left side at base of the broom. This is usually overgrown by sphagnum moss. The broom looks like a tree with systemic infection and usually dies within a few years.*

This point is usually easily determined, since annual rings are normally very narrow on branches.[4] Although it is not certain that the increase starts the same year as infection, the error cannot be great. If *Arceuthobium pussillum* behaves like *A. vaginatum* (Willd.) Presl., a 3- or 4-year lag is possible.

Most infected trees bear more than one infection, and as many as 36 witches'-brooms were found on one tree. On older trees that have been subjected to infection for a long period of time, the older brooms that originated when the tree was young usually are of the leader-type, whereas those of more recent origin are of the bush-type. This appears to substantiate the conclusion that the broom form is largely determined by the vigor of the host.

Definite reinfection of previously infected parts of the host has not been noted. To a casual observer reinfection would appear to occur, since new infection does take place on a witches'-broom caused by a previous infection. Such "reinfection" appears as a small broom on the branchlet of a large broom. No small brooms were ever found on branchlets bearing evidence of previous infection.[5] In some cases the sex of the dwarfmistletoe on the small broom was the opposite of that on the large broom, which definitely establishes that the small broom resulted from new infection.

Influence on Tree Growth and Mortality

The general observation that dwarfmistletoe depresses growth was corroborated by measurements made on a sample of paired infected and healthy trees. This sample indicated that for pole-size trees less than 100 years old, height and diameter growth were reduced by about 26 percent and for trees over 100 years old by about 15 percent. The sample was small, and the witches'-broomed trees had been infected for an unknown and varying portion of their lives. The results therefore are not considered a reliable quantitative measure of the reduction in average annual increment for the period following infection. They give evidence, however, that an appreciable reduction in growth does occur and that the reduction has more serious consequences when relatively young trees are infected.

The large number of dead, heavily witches'-broomed trees, standing or down, in infected stands has convinced us that dwarfmistletoe on black spruce causes con-

[4]A reviewer has pointed out that spruce branches can live for years without laying down annual rings. Therefore, some of the age determinations for witches'-brooms could be low, especially for the old, low-vigor brooms.

FIGURE 5. *Large black spruce killed by dwarfmistletoe. Almost the entire crown consists of numerous bush-type witches'brooms.*

[5]See second paragraph in section on Variations in Witches'-broom Development.

siderable mortality. These dead trees are very often dominants rather than trees in the lower crown classes typical of normal mortality in uninfected stands (Fig. 5). It has been observed in this as well as other investigations (Weir 1916) that a broom often is the last part of the tree to die. On some trees no foliage remained on the "healthy" part of the tree, but a few scattered living needles and mistletoe shoots persisted on a broom.

Gifford (1901) states that dwarfmistletoe causes death by depletion. One factor apparently is concentration of food in the infected branches (Weir 1918); another is the great reduction of leaf surface on older witches'-brooms. Although a single broom may cause mortality in a seedling or small sapling as previously described, larger trees apparently are not killed by a single infection. However, death results in older trees with severe multiple infection and little or no infection-free crown. The more numerous and severe the infections are the sooner trees die after they first become infected. The high concentration of stored food in brooms (Weir 1918), along with the reduction of foliage on older brooms, suggest that infected parts of the tree do not contribute synthesized food to the rest of the tree and, in fact, may utilize food synthesized in "healthy" parts of the tree.

The type of witches'-brooms on a tree appears unimportant in determining how much infection is needed to cause mortality. On larger merchantable-size trees which have the greatest value, however, bush-type brooms predominate. Dying infected trees usually have 75 percent or more of their foliage on infected branches. Most trees, even those with multiple infection, appear reasonably vigorous as long as a considerable amount of infection-free crown is present. In the areas where age determinations were made, the oldest living broom was 45 years old.[6] Infection doubtless had been present much longer than this, as indicated by old dead and down trees bearing evidence of large brooms. Further, the stand characteristics, as well as the type of infection found in these areas, led us to believe that infection had occurred at least as far back as the preceding generation of spruce. Since some of the living trees in the stand were mature, the finding of infections much older than 45 years would be expected unless the host is killed before infections acquire greater age.

[6]Possibly the broom was older; see footnote 4.

Summary

There are marked variations in host reaction to dwarfmistletoe infection of black spruce. Almost all infections cause the formation of witches'-brooms. The very few infections that do not form brooms apparently are of little consequence. The form of brooms seems to be determined by host vigor and age. The brooms are of three types, called bush-type, leader-type, and weak-type as indicative of their characteristics.

On very young trees infection can result in complete elimination of the original tree, leaving a tree-shaped, leader-type witches'-broom that gives the erroneous impression of systemic infection. For the first 5 to 10 years brooms grow very rapidly, and the dwarfmistletoe produces much seed. An abrupt decline in vigor follows. The age of a broom can be determined by examining the annual rings on infected branches and noting the period of marked growth stimulation. Infections cause a marked decline in trunk growth, especially in younger trees. The disease also causes considerable mortality. Dying trees usually have 75 percent or more of their foliage on infected branches. In the areas examined, older trees survived as long as 45 to 50 years following infection with dwarfmistletoe.

Literature Cited

ANDERSON, RALPH L., and FRANK H. KAUFERT. 1953. The control of dwarfmistletoe on black spruce. Univ. Minn. Sch. Forestry. For. Note 13, 2 pp., illus.

(Processed.)
DOWDING, E. S. 1929. The vegetation of Alberta. 3. The sandhill areas of central Alberta with particular reference to the ecology of *Arceuthobium americanum*. J. Ecol. 17:62-105.
FREEMAN, E. M. 1905. Minnesota plant diseases. Rpt. of the Surv. Bot. Ser. 5, 432 pp., St. Paul, Minn.
GIFFORD, J. 1901. The dwarfmistletoe, *Razoumofskya pusilla*. Plant World 4: 149-150.
GILL, L. S. 1935. *Arceuthobium* in the United States. Trans. Conn. Acad. Arts Sci. 32:111-245. Also by Yale Univ. Press.
HEDGCOCK, G. G. 1915. Notes on some diseases of trees in our national forests. V. Species of *Razoumofskya* (*Arceuthobium*) attacking Gymnosperms. Phytopathology 5:175-181.
HEINRICHER, E. 1918. Die Bedingungen, unter denen durch den Parasitismus der Zwergmistel (*Arceuthobium oxycedri*) auf *Juniperus* Hexenbesen entstehen können. Z. Pflanzenkrankh. 28: 193-200.
HIMMEL, W. J. 1935. A case of change of tropic response. Plant Physiol. 10: 196-197.
KORSTIAN, CLARENCE F., and W. H. LONG. 1922. The western yellow pine mistletoe: effect on growth and suggestions for control. U.S. Dept. Agr. Bull. 1112, 36 pp.
KUIJT, JOB. 1955. Dwarfmistletoe. Bot. Rev. 21:569-627.
POMERLEAU, R. 1942. Le gui de l'epinette noire dans le Quebec. Nat. Canad. 69(1):11-31.
VON SCHRENK, H. 1900. Notes on *Arceuthobium pusillum*. Rhodora 2:2-5.
WEIR, J. R. 1916. Mistletoe injury on conifers in the Northwest. U.S. Dept. Agr. Bull. 360, 39 pp.
———. 1918. Effects of mistletoe on young conifers. J. Agr. Res. 12: 715-718.

Methods of Vegetation Study

By Edwin Allen Phillips. A Holt-Dryden Book. Henry Holt and Company, Inc. New York 17. 107 p. $2.95.

Review by Stephen H. Spurr
The University of Michigan

This brief field manual summarizes many techniques of interest to forest biologists. Prof. Phillips of Pomona College and The University of Michigan Biological Station has prepared a useful survey of synecological techniques designed for the beginning student in plant ecology.

The book is catholic in its approach, giving equal weight to American and European classification schemes and measurement practices. Short chapters, ranging upwards from a page in length, discuss floristic measurement, including frequency, abundance and density, cover and basal area, transects, and plotless methods. The study of succession is covered in nine pages. The major part of the book is concerned with the synthesis of data from different stands, presenting methods drawn from statistical procedures used by American ecologists and European plant sociologists.

To the forester the book may well seem quite elementary. Methods are presented empirically and factually, with little attention being given to the reasoning behind the technique or the interpretation of the results. Yet the writing is clear, key references are given, and the book will prove useful in fulfilling its purpose of supplementing an ecology textbook in a field course dealing with plant communities.

Natural Emplacement of Dwarfmistletoe Seed on Ponderosa Pine

BY
LEWIS F. ROTH

RECENT INVESTIGATIONS (Roth 1953) of dwarfmistletoe (*Arceuthobium campylopodum* f. *campylopodum* (Engelm.) Gill) in the ponderosa pine (*Pinus ponderosa* Laws.) forests of the Deschutes Plateau in central Oregon indicate that the distribution of the pest is not based on chance alone. In an attempt to determine what factors regulate the occurrence of dwarfmistletoe the apparent relationship between seed dispersal and dwarfmistletoe prevalence appeared great enough to warrant a study of the seeding habits of the plant. It soon became apparent that the usual understanding of dwarfmistletoe seed dispersal is based on incomplete knowledge of the process. The studies described here fill in some of the gaps in the information.

Forceful discharge of the adhesive dwarfmistletoe seeds from distended, elastic fruits and the eventual germination of the seeds on the host branches are well described (Heinricher 1915, Peirce 1905, Johnson 1888, Weir 1918, Dowding 1929, Kimmey 1957, Gill 1935, 1954, Gill and Bedwell 1949). However, between these events important steps occur which apparently are unreported. Most observers appear to have accepted the stems as the initial as well as the final resting place of the seeds that ultimately result in infection. This conclusion does not hold where ponderosa pine is the host. Peirce (1905) reported seeds of *A. occidentale* Eng. on pine needles, and the idea that seeds adhere to the first object they strike is sometimes conveyed.

Dwarfmistletoe plants usually are located within the tree crown on the bare parts of the branches some distance from the foliage. From this position initial seed flight is unhampered by surrounding needles. However, during the period of seed discharge examination of branches in the vicinity of dwarfmistletoe plants revealed very few seeds adhering to branch parts that were bare of needles. It was found experimentally that hard smooth surfaces such as pieces of plywood or even plant drying blotters when held close to mature plants were poor receptors for seed collection because the seeds glanced after striking. Apparently the non-foliated stems act similarly. On the other hand, pine needles a few feet from fruiting plants were observed to accumulate numerous seeds.

This differential in seed interception by stems and by needles appears to be determined by the adhesiveness of the viscin layer (the outer coating of the seed), the velocity of seed in flight and the rigidity of the intercepting surface. At the instant of discharge the seeds are traveling at high velocity. They are wet with cell sap and are only moderately sticky. These conditions persist only during the first instant of flight and if the surface struck is rigid as in the case of the older stems, the seeds tend to glance. On the other hand the resilient needles yield to the impact and are more

---

The author is Professor of Botany and Forest Pathology at Oregon State College, Corvallis, and Collaborator, U. S. Forest Service, Division of Forest Disease Research. Technical paper No. 1222 Oregon Agric. Expt. Sta.

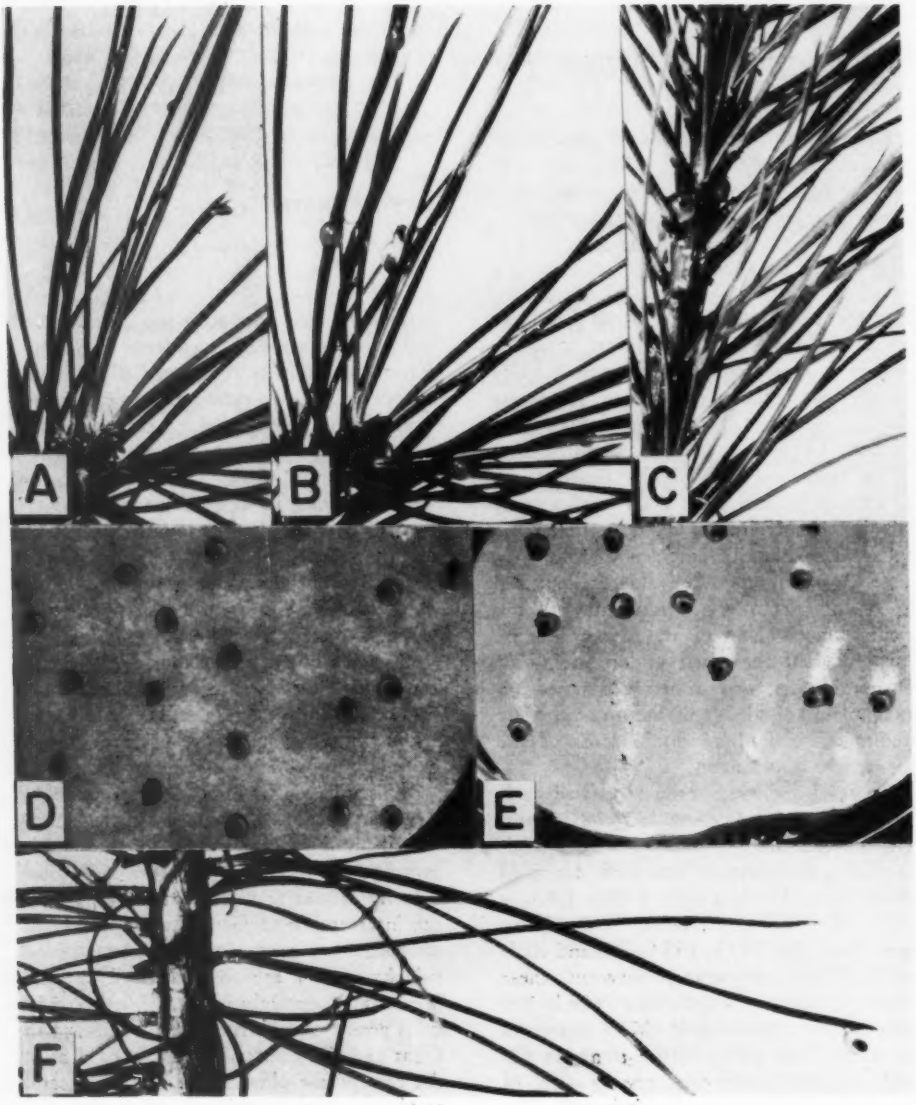


FIGURE 1. *Steps in interception and emplacement of dwarf mistletoe seeds on ponderosa pine. A. Freshly discharged and intercepted seeds. B. The same seeds after an hour of light rain. C. and F. Similar seeds after four hours of light rain. D. Seeds with viscin distended by water imbibed from a wet filter paper. E. Seed movement on a vertically supported filter paper functioning as a wick. Glistening viscin tracks mark the path of seed movement.*

likely to intercept the seeds. The adhesiveness of the seeds appars to increase rapidly even within the interval of flight. Seeds that have traveled more than a few feet are quite sticky. They decelerate rapidly and thus are more liable to adhere.

Most of the seeds remain on the needles at the point of interception (Fig. 1A) until the first wetting rain. But during prolonged dry periods following discharge some loss of adhering seeds results from wind and weathering.

The viscin layer absorbs water readily when moistened and, swelling to many times its original size, becomes slippery (Fig. 1). The distended bead-like seeds (Fig. 1D) gain considerable mass from the water held by the viscin and as a result begin to slide along the needles. Movement is facilitated by a viscin fraction which lubricates the surface over which the seeds slide and is dissipated in the process (Fig. 1E). Seeds lodge most often against the stems in the axil of the fascicle or against the open end of the fascicle sheath. However, if the needle is inclined downward they usually slide from the needle tip (Fig. 1F) and are lost.

If the amount or duration of rainfall is inadequate to cause the seeds to slide all the way to the stem they dry down and adhere tightly to the needles until a subsequent rain when they slide again. This process is not repeated indefinitely, however. Ordinarily after two to four rains, the lubricating viscin is washed away and the seeds, wet or dry, are held in place by fibrillose viscin strands.

Viscin is not uniformly distributed over the seed but is thickest just back of the pointed end (Fig. 1D). The broad end is free of the adhesive. This distribution appears to shift the center of gravity of the wet seed toward the pointed end which causes the seed to orient itself point first as it slides down the needle. Usually the point of the seed is drawn into the axil of the fascicle upon drying (Fig. 2) so that when germination occurs the primary root is directed into the axil. The root of a seed

FIGURE 2. *Dwarf mistletoe seeds lodged on the stem and in fascicle axils against the stem of ponderosa pine. The embryo end of the seed becomes directed toward the axil as the viscin dries. Fibrillose viscin strands hold the seed in place.*

lodged against the open end of the needle sheath frequently is directed into the sheath.

Heavy rains that occur soon after seed discharge may wash some seeds down the stems onto older wood where infection is less likely (Rocky Mountain Forest and Range Experiment Station, 1957); however, large numbers do not appear to be removed in this way. Amounts of precipitation supporting seed movement lie roughly between 0.25 and 2.0 inches. Individual rains exceeding this maximum, which would wash the seeds away, are unusual in the study area.

This history of movement of all seeds intercepted by 15 branchlets of the middle and lower crown of a 12-foot ponderosa pine sapling was recorded during two seasons. The seeds were discharged from a dwarfmistletoe plant on the main stem of the tree. Possibly a few came from a more distant source. The first fall rain in 1957, 1.43 inches, occurred at the peak of dwarfmistletoe seed discharge, and was followed by an extended rainy period. In 1958 little rain occurred until dwarfmistletoe seed discharge was complete (Fig. 3).

In 1957 a cumulative total of 93 seeds was counted on the tree. The maximum seed accumulation at any one time reached 80 seeds on September 26. Heavy rains during the period September 26 to October 8 washed some seeds from depressed needle tips before thy could be counted. The esti-

mated total interception in 1957, allowing for those washed off without being counted, was 100 seeds. As they were discharged none of these seeds penetrated the mantle of needles surrounding the foliated parts of the stems even though the tree was sparsely foliated. The first rain caused a distinct redistribution of the 80 seeds. Only 34 remained on the tree the day following the rain; 46 had been washed to the ground. Of the 34 remaining, 20 were still on the needles but 14 had been transferred to the stems, mostly in the fascicle axils.

Seed discharge continued for about two weeks, which were unseasonably rainy. Some further seed accumulation resulted. The total number of seeds on the tree increased to 47. However, the rains so facilitated seed movement from the needles that the increase was reflected primarily on the stems in the fascicle axils. For the remainder of the fall season after October 5 there was little change in the number of seeds adhering to the tree except for a slight decrease from the needles. The number on the stems remained nearly constant in spite of several heavy rains in November. During the winter period, probably as a result of mechanical attrition by snow and ice, a sharp loss took place from the needles when the 22 seeds were reduced to 9. No such loss occurred from the stems during this period.

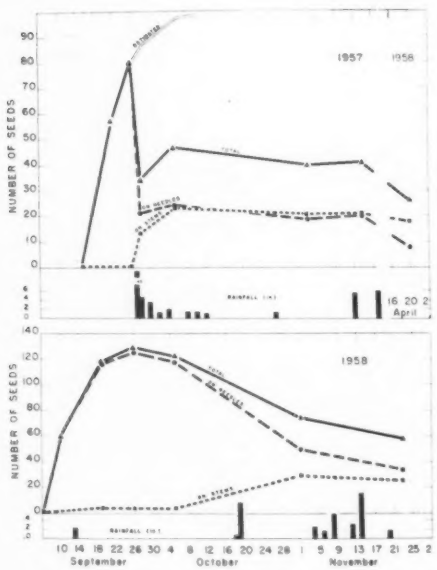


FIGURE 3. *Interception and retention of dwarf mistletoe seeds by a ponderosa pine sapling in 1957 and 1958.*

In 1958 rains adequate to cause significant seed movement were delayed until late October. By that time the discharge of dwarfmistletoe seed was complete. A total of 130 seeds accumulated, again all on the needles. A 0.21-inch rain on September 13 transferred a few seeds to the stems and fascicle axils after which the number remained constant for a month. The peak accumulation on the tree as a whole was recorded on September 26. Seed accumulation from the limited and decreasing discharge following September 26 was more than offset by wind removal of the very dry seeds. A decline in total number of seeds occurred during late September and the first two weeks of October even though no rain fell during that period.

A heavy rain on October 19 accomplished the principal transfer of seeds from the needles. This transfer would appear graphically in Figure 3 as an abrupt break, 122 seeds reduced to 74, like that of September 29, 1957 were it not for the fact that the 1958 counts were made quite some time before and after the rain. As in 1957, after this major movement (reflected in the count of November 1) there was some loss of seeds from the foliage but very little change in the number adhering to the stems, even though November was exceptionally wet. The number of seeds remaining on the stems were approximately the same at the last count of the season both years. This tendency of the tree each season to retain a rather consistent percentage of the intercepted seeds, in spite of wide fluctuations in precipitation, suggests that the level of seed retention is strongly influenced by tree characteristics.

Discussion and Summary

Needles of ponderosa pine rather than stems are the primary interceptors of dwarf mistletoe seeds. An effective biological adaptation brings the seeds into contact with stem tissues of the most susceptible age and also positions the seeds on the stems, usually in the axil of the fascicle, or at the fascicle opening. Apparently both locations are highly favorable for penetration by the primary root of the parasite.

This adaptation seems essential to survival of pine dwarfmistletoe. Naked stems in a position to be hit by flying seeds offer a relatively small target; they retain the seeds poorly and are too old to be readily infected. Foliated stems in themselves present even smaller targets and are so clothed with needles that direct stem hits seldom occur. On the other hand, the numerous and widely spreading needles offer a target of great area and because of their individual flexability they are ideally suited to seed interception. As a result of their large numbers and distribution they literally screen the seeds from the air. At this point a means of transferring the seeds from the needles to the susceptible stem becomes necessary. This is provided by movement attending gelatinization of the viscin during rainy weather.

On the tree studied for this report approximately 20 percent of the seeds had been transferred to the twigs by the end of the year. Twenty-five percent remained on the needles and 55 percent were washed off or otherwise removed.

This movement of the seeds appears significant when considered with respect to the branching and foliar characteristics of the tree. Ponderosa pines vary widely with respect to these characteristics. In the juvenile stages all intergrades are found between trees with long drooping needles and small, sometimes pendent, branches and trees having an erect branching habit and erect, rigid needles. It appears likely that trees of the latter type would transfer a higher percentage of intercepted dwarf mistletoe seeds to the susceptible stems and thereby would be more liable to damage by the parasite.

Literature Cited

DOWDING, E. S. 1929. The vegetation of Alberta. III. The sandhill areas of central Alberta with particular reference to the ecology of *Arceuthobium americanum* Nutt. Jour. Ecol. 17: 82-105.

GILL, LAKE S. 1935. *Arceuthobium* in the United States. Trans. Conn. Acad. Arts and Sci. 32: 111-245.

————. 1954. Dwarf mistletoe of Ponderosa Pine in the Southwest. Station Paper 14. Rocky Mountain Forest and Range Experiment Station. 9 pp. processed.

————, and JESS L. BEDWELL. 1949. Dwarf mistletoe. U. S. Dept. Agriculture Yearbook-Trees 1949. 458-461.

HEINRICHER, E. 1915. Beiträge zur Biologie der Zwergmistel, *Arceuthobium oxycedri*, besonders zur Kenntnis des anatomischen Baues und der Mechanik ihrer explosiven Beeren. Sitzungsber. Akad. Wiss. Wien Abt. 1., 124 Band, 3. and 4. Hefte.

JOHNSON, T. 1888. *Arceuthobium oxycedri*. Ann. Bot. 2: 137-160.

KIMMEY, J. W. 1957. Dwarf mistletoes of California and their control. Technical Paper 19. California Forest and Range Experiment Station.

PEIRCE, GEORGE J. 1905. The Dissemination and Germination of *Arceuthobium occidentale*, Eng. Annals of Botany 19: 99-113.

ROCKY MOUNTAIN FOREST AND RANGE EXPERIMENT STATION 1957. Forest Disease Research. In Annual Report 1957. 111 pp. processed.

ROTH, LEWIS F. 1953. Pine Dwarfmistletoe on the Pringle Falls Experimental Forest. Research Note 91. Pacific Northwest Forest and Range Experiment Station.

WEIR, J. R. 1918. Experimental investigations on the genus *Razoumofskya*. Botanical Gazette 66: 1-31.

Bias Due to Edge Effect in Using The Bitterlich Method

BY
TOSHIRO HAGA
KANJIRO MAEZAWA

ONE OF THE DIFFICULTIES in using the Bitterlich method (Bitterlich, 1948) is how to treat sample points that are selected near the tract boundary. Regarding this problem, Husch (1955, 1956) and Grosenbaugh (1955) have exchanged views. Husch asserted that sample points should be selected within the line which is drawn some distance D inside the area. On the other hand, Grosenbaugh argued that according to Husch's method a definite edge effect bias might be introduced, and proposed a practical procedure sweeping only the interior 180°, 120°, 90° or 60° with the angle-gauge at all points near the boundary. Each count so made would then be multiplied by 2, 3, 4, or 6. The latter is a very interesting suggestion, but further study seems necessary in the application of the constants.

Several years ago Masuyama (1953) stated "The Condition of Unbiasedness" in regard to the subject in general and threw theoretical light on this difficulty. According to his theory, bias would arise in the Bitterlich method if sample points were selected only within the forest land area when a part of the enlarged circle extended outside the area.

In this paper, the writers present the general formula for obtaining an approximate value of the bias and compare estimated values based on it with actual measurement obtained by desk experiment.

How Bias Enters in

Various tree cross-sections at breast height are contained within the area T (Fig. 1), the total basal area is denoted by g, and the total area of enlarged circles having p times diameter of each diameter is shown by G. Further, the number of sample points selected at random in T is denoted by N, and the number of enlarged circles which are contained at the i-th sample point is denoted by n_i ($i = 1, 2 \ldots N$). Then g can be estimated by using G divided by p^2 because $\bar{n}T$ is nearly equal to G (Grosenbaugh, 1952).

$$G \doteqdot \bar{n}T \qquad (1)^1$$

$$g = G/p^2 \qquad (2)$$

where $\bar{n} = \Sigma n_i/N$.

If a part of the area of the enlarged circle extends outside of T, $\bar{n}T$ would become an unbiased estimate of G_0 which shows a partial area of G contained within T, and g would have a bias. In such a case it would be necessary to consider an ex-

[1]Formulae are given identifying numbers in order to facilitate reference at various points in this article.

The authors are with the Sanyo Pulp Co., Ltd., and the Tokyo University Forests, Tokyo, Japan.

tended area T' which contained all areas of the enlarged circles (Fig. 1).

Now each tallied number at the i-th sample point selected at random in T' is denoted with n_i'. Then the mathematical expectation of the mean value $\bar{n}'$, $E(\bar{n}')$, is given as follows:

$$E(\bar{n}') = G/T'. \qquad (3)$$

From the above formula, G would be estimated as

$$\hat{G} = \bar{n}'T' \qquad (4)$$

where $\hat{G}$ means the estimate of G.

On the other hand, if n_i is counted in the original forest land area T, as in the above case, then

$$E(\bar{n}) = G_b/T. \qquad (5)$$

From the above formula, G_b would be estimated as

$$\hat{G}_b = \bar{n}T, \qquad (6)$$

and it would not agree with the preceding formula (Husch, 1955; Grosenbaugh, 1955).

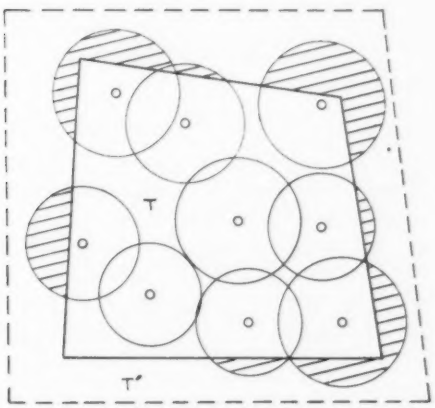


FIGURE 1. *An explanation of edge effect bias. The area T surrounded by solid line is the forest land area. The area T' surrounded by broken line is the extended area.*

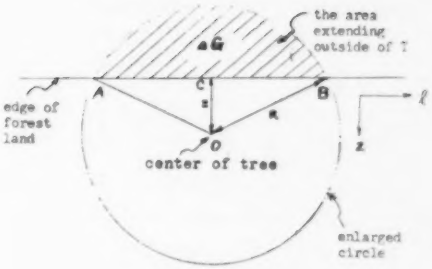


FIGURE 2. *Illustration of Formula (14).*

Then the bias ΔG on the enlarged circle area given as

$$\Delta G = G - G_b \qquad (7)$$

is the area of G that extends outside of T.

Therefore, basal areas corresponding to the difference ΔG would become the bias b on basal area, and g would be underestimated as small as b.

$$b = \Delta G/p^2. \qquad (8)$$

Estimation of the Bias

Let us now consider the case whereby only one tree is contained within the forest land area T, and let the radius of its enlarged circle be R (= pr). Further, let that part of the enlarged circle outside of T be ΔG (see hatched part in Figure 1).

In the area T, ΔG has a positive value only in the neighborhood of the edge of the forest land, and it will be zero near its center. Let us suppose axis l is on the margin and axis z is vertical to it (Fig. 2). Here, it is assumed that the margin is essentially a straight line.

When the center of the tree falls inside at a distance z from the edge, ΔG is developed as follows.

In Figure 2

$$\cos(\angle AOB/2) = z/R$$

and $$\angle AOB = 2\cos^{-1}(z/R).$$

Then the sector OAB is shown as

$$\text{sector OAB} = R^2 \cdot \angle\, AOB/2 = R^2 \cos^{-1}(z/R). \quad (9)$$

On the other hand, the isosceles triangle OAB is shown as

$$\text{triangle OAB} = OC \cdot AB/2 = z\sqrt{R^2 - z^2}. \quad (10)$$

Then, ΔG, the hatched area, is given by the difference of (9) and (10), i.e.,

$$\Delta G = R^2 \cos^{-1}(z/R) - z\sqrt{R^2 - z^2}. \quad (11)$$

If the tree falls at random within T, the mathematical expectation of ΔG, $E(\Delta G)$, is developed as follows.

Let us suppose that the area T is covered with a grid (with the length of δz and the width of δl), and that the total number of crossed points of the grid in area T is N. Further, suppose that the tree falls at random at each crossed point and let ΔG for the trees at i-th crossed points be ΔG_i.

When the center of the tree falls at all crossed points, the average value of ΔG will be shown as

$$\overline{\Delta G} = \sum_{i=1}^{N} \Delta G_i / N \fallingdotseq \Sigma \Delta G_i \delta z \delta l / T. \quad (12)$$

As the mathematical expectation of ΔG is defined as the limiting case of $\overline{\Delta G}$, where the mesh of the grid becomes infinitesimally fine, summation in the formula (12) is replaced by integration

$$E(\Delta G) = \iint_T \Delta G \, dz \, dl / T \quad (13)$$

where $\iint_T$ means an integration within the area T. The integration in formula (13) is explained below.

As mentioned before, the value of ΔG is largest when the tree is at the edge, when it is equal to one half of the area of the enlarged circle. The value is zero when the tree is remote from the edge. Since the radius of the enlarged circle is R and the total length of the perimeter is L, it will be necessary to integrate from zero up to R on axis z and to integrate all length around perimeter L on axis l.

Then the integration in formula (13) is shown as

$$\begin{aligned} \iint_T \Delta G \, dz \, dl &= \int_L \int_0^R \Delta G \, dz \, dl \\ &= \int_L \left[\int_0^R R^2 \cos^{-1}(z/R) \, dz - \int_0^R z\sqrt{R^2 - z^2} \, dz \right] dl \\ &= \int_L (R^3 - \tfrac{1}{3}R^3) \, dl \\ &= \tfrac{2}{3} R^3 L \end{aligned} \quad (14)$$

then $E(\Delta G)$ is given as

$$E(\Delta G) = 2R^3 L / 3T \quad (15)$$

where L means the length of the edge (i.e. perimeter) of the forest land.

As the formula (15) applies only where one tree falls within T, let us consider the general formula for the ordinary case where many trees are so located. Since $E(\Delta G)$ in this case is given as summation of $E(\Delta G)$ of each tree in preceding case, then

$$\begin{aligned} E(\Delta G) &= \Sigma E(\Delta G_j) \\ &= \Sigma 2R_j^3 L / 3T \\ &= \frac{2L}{3T} \Sigma R_j^3 \\ &= \frac{2Lp^3}{3T} \Sigma r_j^3 . \end{aligned} \quad (16)$$

On the other hand, the total area of enlarged circle G is given as

$$G = p^2 \Sigma \pi r_j^2 . \quad (17)$$

Since G is underestimated by ΔG on the average when the condition of unbiasedness is neglected, the relative bias e is calculated as

$$e_{cal} = b/g = \Delta G / G \quad (18)$$

$$= 2Lp \Sigma r_j^3 / 3\pi T \Sigma r_j^2 \quad (19)$$

$$= f \cdot 2Lp\bar{r} / 3\pi T \quad (20)$$

where $\bar{r}$ is a mean radius of the trees composing objective stand.

The factor f in the formula (20) is a function of the variation in tree radius and is expressed as follows:

$$f = 1 + \left(\frac{\sigma_r}{\bar{r}}\right)^2 + \ldots \quad (21)$$

In practice, if the variation is small, i.e., $\sigma_r/\bar{r}$ is nearly equal to zero, f can be approximated by one.

The above mentioned formulas (19) and (20) give an appropriate value of the relative bias under the following assumptions:

1. The edge of the forest land is not so irregular but that it can be considered as a straight line. The effect of corner on bias is not considered because it is negligibly small.

2. Stand density is homogeneous both in the marginal and central area of forest land.

Formula (14) was developed for trees growing at the edge and z was therefore integrated from 0 to R. For trees growing inside, integration would be from ϵ to R, where ϵ is the distance between the position of trees and the edge. The relative bias in this case would be smaller than that given by the formula (19). Therefore, it is seen that formula (19) gives the upper limit of relative bias.

An Example

The validity of the approximate formulas on relative bias obtained in the preceding section was tested by using a stand map reduced to the scale of one fiftieth. Because of the need for exact measurements a desk experiment was considered to be more appropriate than a field survey. Such slight discrepancies as would occur would not be very important for this kind of test.

The stand studied had been artificially regenerated, and was even-aged. It was composed of *Cryptomeria japonica*, 31 years old, with a mean diameter of about 15 cm (6 inches) and a mean height of about 13 m (43 feet). The forest land area T was 2049 sq m (0.506 acres) and its circumference was 182.55 m (0.113 miles). Moreover, 584 trees were contained in it. The number of trees classified by diameter is shown in Table 1.

The total basal area based on actual measurements of diameter at breast height on each tree, considered as the true value in these experiments, was 10.745 sq m (115.62 square feet).

The map was first covered with the grid 4 cm x 4 cm, the crossed points being considered as the sample points in this experiment. This distance of 4 cm corresponds to 2 m in the field survey.

The total number of sample points N located within the forest land area T was 528. After drawing enlarged circles, 50 times the diameter of each tree at breast height, for each tree cross-section, the tallied numbers at each sample point were counted. The total count was 6371.

Since

$$\Sigma n_i = 6371, N = 528$$

$$\bar{n} = 12.07, T = 2049\,m^2$$

G_b is obtained as

$$\hat{G}_b = 24730\ m^2$$

TABLE 1. Number of trees classified by diameter.

D.b.h. class (cm)	Number of trees
6	1
8	20
10	69
12	103
14	106
16	116
18	94
20	45
22	19
24	6
26	4
28	1

by the formula (6). Then, g_b is obtained as

$$\hat{g}_b = \hat{G}_b/p^2 = 9.892\,m^2.$$

These are the bias estimates.

The bias b and the relative bias e are obtained respectively as follows:

$$\hat{b} = 10.745 - 9.892 = 0.853$$

$$e_{obs} = \hat{b}/g = 0.079.$$

The standard deviation of e_{obs} is obtained as follows. From the tallied numbers n_i at each sample point, the mean square $V(n_i)$ is calculated. The value in this case is

$$V(n_i) = \Sigma(n_i - \bar{n})^2/(N-1) = 9.34.$$

Under the above value, the standard deviations σ_G and $\sigma_{e_{obs}}$ on G_b and e_{obs} are obtained respectively as follows:

$$\hat{\sigma}_G = \sqrt{V(n_i)/N}\,T = 272.5$$

$$\hat{\sigma}_{e_{obs}} = \hat{\sigma}_G/G = 0.010.$$

The same experiments were made for each case where p square was 400, 1000, 5000, and 10000. From 30 to 100 sample points selected at random from the preceding 528 points were used in these experiments. The results are summarized in Table 2.

An area T', containing the enlarged circles extending outside of T, was drawn on a map. This was covered by the grid as in the preceding case. Both the shape and size of T' were chosen for ease of calculation and to keep the size as small as possible because there are no theoretical restrictions on them.

The objective area T' calculated from the map was 2964 sq m and 741 sample points were contained in it. Since 6739 trees were counted as the total tallied number, G is obtained as

$$\hat{G} = 6739 \times 2964/741 = 26950\ m^2$$

by the formula (2). Then

$$\hat{g} = 10.780\ m^2.$$

These values are the unbiased estimates of G and g, and they are close to the true values 26890, and 10.745 sq m respectively.

The approximate value of relative bias e when p square is 2500 is calculated by putting the actual values, such as

$$L = 182.55\,m, T = 2049\,m^2,$$

$$\Sigma r_j^3 = 0.2886\,m^3, \Sigma r_j^2 = 3.453\,m^2$$

TABLE 2. Results of experiments and comparison between e_{obs} and e_{cal}.

(1) p	(2) p^2	(3) N	(4) Σn_i	(5) $\hat{g}_b$	(6) $\hat{b}$	(7) e_{obs}	(8) e_{cal}	(9) $V(n_i)$	(10) $100\sigma_{e_{obs}}$	Basal area factors in square feet per acre
				m^2	m^2	*percent*	*percent*			
20	400	100	209	10.70	0.05	0.5	3.2	1.18	5.2	108.9
31.6	1000	100	513	10.51	0.24	2.2	5.0	2.46	3.0	43.6
50	2500	528	6371	9.89	0.85	7.9	7.9	9.34	1.0	17.4
70.7	5000	100	2334	9.56	1.18	11.0	11.2	32.91	2.2	8.7
100	10000	30	1362	9.30	1.44	13.4	15.8	109.97	3.7	4.35

(1) p: Ratio of diameter magnification. (3) N: Number of sample points. (4) Σn_i: Total of tallied numbers. (5) $\hat{g}_b$: Biased estimate of basal area. $\hat{g}_b = \Sigma n_i\,T/N\,p^2$. (6) b: Estimate of bias on g. $\hat{b} = g - \hat{g}_b \cdot g = 10.745\ m^2$. (7) e_{obs}: Relative bias estimated by experiment. (8) e_{cal}: Relative bias calculated by equation (19). (9) $V(n_i)$: Mean square of tallied number. (10) $\sigma_{e_{obs}}$: Standard deviation of e_{obs}.

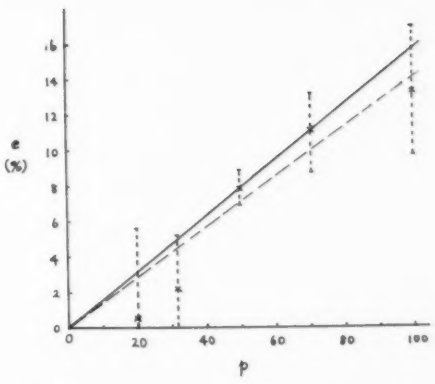


FIGURE 3. *Comparison between observed e and calculated e for various values of p. Solid line based on equation (19) and broken line on equation (20) with f = 1.*

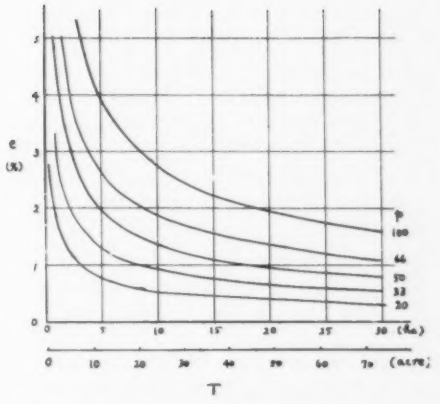


FIGURE 4. *Relationship between e_{cal} and T in cases where p is 20, 33, 50, 66, and 100. Conditions (1) r̄:10 cm; (2) shape of forest land: square.*

in the formula (19). Namely,

$$e_{cal} = \frac{2 \times 182.55 \times 50 \times 0.2886}{3 \times 3.142 \times 2049 \times 3.453} = 0.079.$$

This value very closely agrees with the value previously obtained by actual measurement, i.e., $e_{obs} = 0.079$.

The results where p^2 is 400, 1000, 5000 and 10000 were compared in columns 7 and 8, Table 2. These values for each p are very close to the measured ones within the ranges of the estimated error on them (column 10). Figure 3 shows the above comparison graphically in which the vertical broken lines denote the sizes of $\hat{\sigma}e_{obs}$. As relative bias is proportional to the values p, the relationship between e and p is shown as a straight line through the origin. The broken line corresponds to the formula (20) in which f is given as one (Fig. 3).

Interpretation

Figure 4 shows the relationship among e, p and T under the following conditions: (1) the values of r and f in the formula (20) are 10 cm and 1, respectively, and (2) the shape of the forest land is square.

The following explanation should be adequate due to the obtained formulas and the above shape. The bias will become negligibly small as a forest land grows

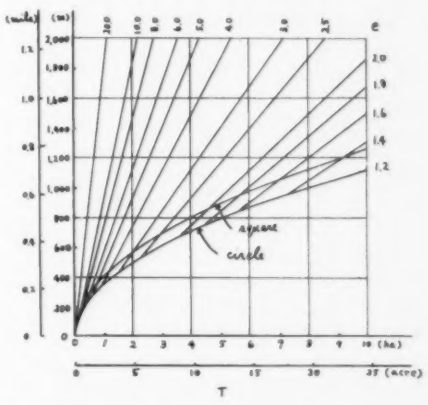


FIGURE 5. *Relationship among L, T, and e, when p = 50, and r = 10 cm or when p = 20 and r = 25 cm. The two parabolic lines through the origin correspond to perimeter in relation to area for the square and circle and the radiating lines for e terminate at the lower parabola because a circle has the smallest possible perimeter for a given area.*

larger. Thus the Bitterlich method can be used without consideration of the edge effect bias, when the land under consideration is not elongated or irregular in shape or not particularly small in area. Edge effect bias should be considered when the area of land is small or the edge is long. Then the relative bias can be estimated beforehand from Figure 5, where p and r are chosen as 50 and 10 cm respectively. As relative bias is proportional to both p and r, relative bias for other p and r values can be obtained by multiplying by ratios. For example, if $p = 31.6$ ($p^2 = 1000$), $r = 20$ cm, $T = 7$ ha, and $L = 1200$ m, the value of e in Figure 5 for the given T and L values is 1.85 percent and the relative bias for the example is obtained as follows:

$$1.85 \times \frac{31.6}{50} \times \frac{20}{10} = 2.34 \text{ percent}$$

(Figs. 4 and 5.)

Literature Cited

BITTERLICH, W. 1948. Die Winkelzählprobe, Allgemeine Forst-und Holzwirtschaftliche Zeitung 59:4-5.

HUSCH, B. 1955. Results of an investigation of the variable plot method of cruising. J. For. 53:570-578.

———. 1956. Comments on the variable plot method of cruising. J. For. 54:41.

GROSENBAUGH, L. R. 1952. Plotless timber estimates. J. For. 50:32-37.

———. 1955. Comments on "Results of an investigation of the variable plot method of cruising." J. For. 53: 734.

MASUYAMA, M. 1953. A rapid method of estimating basal area in timber survey. Sankhyā 12:291-302.

SANTALO, L. A. 1953. Introduction to Integral Geometry, Hermann & Cie Editeurs. Paris.

The Secondary Phloem of Douglas-Fir

BY
STEVE J. GRILLOS
FRANK H. SMITH

THE ANATOMY of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) has been intensively investigated in recent years with regard to certain features of development. Allen (1946, 1947a, 1947b) described fertilization, embryogeny and development of the apical meristems, Crafts (1943) and Sterling (1946, 1947a, 1947b) discussed the structure and development of the stem apex, buds and young stems, and Smith (1958) described the structure and development of the hypocotyl of the seedling.

The secondary xylem has been investigated many times, but the anatomy of the secondary phloem had been neglected until Chang (1954) made a survey study of the bark structure of North American conifers and included a brief description of the secondary phloem of Douglas-fir. Shimakura (1936a) described fibrous sclerotic cells in the phloem of *Pseudotsuga japonica* Beissn., and also the expansion of phloem parenchyma in the outer phloem of Douglas-fir and other conifers (1936b).

The development of the vascular cambium and structure of the secondary phloem of pine (Abbe and Crafts, 1939) and redwood (Isenberg, 1943) has been studied in more detail. Holdheide (1951), Huber (1939, 1949) and Bannan (1955) have discussed the secondary phloem and its seasonal development in various conifers other than Douglas-fir.

Materials and Methods

Samples of bark with or without a small amount of adjacent xylem were collected from the trunks of trees of various ages near Corvallis, Oregon during 1955. Most of the trees were growing on south slopes at an elevation of approximately 600 feet, and ranged in age from 1 to 200 years but mostly from 25 to 35 years. Collections were made at weekly intervals during the growing season and at 2- or 3-week intervals during the rest of the year. The samples were trimmed to approximately ¼ x ½ x ½ inch in size, with a jeweler's hacksaw and razor blade, so that ½ x ½ inch sections in cross, radial and tangential planes could be obtained from each sample.

Several killing solutions were used but Randolph's modification of Navashin's solution gave the best results. Air was evacuated from the samples when they were placed in the killing solution where they were left for 3 days. The samples were then washed in running water, bleached with a 15 percent hydrogen peroxide solution, dehydrated and embedded in 56°-58° C Tissuemat following the tertiary butyl alcohol-paraffin oil series of Johansen (1940). The embedded samples were soaked in a solution of glycerin and a detergent (Alcorn and Ark, 1953) for one month at approximately 37° C after which they could be sectioned immediately, or

---

This paper is taken in part from a thesis presented by the senior author (now located at Modesto Junior College) to Oregon State College, Corvallis, Oregon, in partial fulfillment of the requirements for the Ph.D. degree. The junior author is Professor of Botany at Oregon State College. This is Research Paper No. 360 of that institution.

stored in water in a refrigerator until needed. Sections were cut at 8 to 20μ on a rotary microtome. Better sections were obtained when the blocks were cooled directly with carbon dioxide under pressure just before cutting. The sections were stained progressively with safranin and hematoxylin. Resorcin blue was also used to stain callose deposits, ferrous sulphate for tannins, and cupric acetate for resins (Johansen, 1940).

The paraffin technique used here is not adequate for the preservation of cork and most of the mature cork cells in the preparations were collapsed.

Vascular Cambium

The use of the term cambium has been carefully reviewed by Bannan (1955). Cambium is used here as by Bannan in his study of *Thuja*. That is, cambium is used to indicate not only the initiating layer of cells but also the zones of undifferentiated or dividing xylem and phloem mother cells on either side. These zones of mother cells may be very narrow when the cambium is dormant, or extremely broad when the cambium is undergoing active periclinal divisions (Fig. 1). Cytological details of cambial divisions in conifers have been described by Bailey (1920). Since observations made here are in agreement in all respects, discussion of such details has been omitted.

The number of cell layers in the dormant cambium of Douglas-fir is variable not only from tree to tree but also on different sides of the same tree. The dormant cambium may consist of as few as two layers of cells, but usually consists of 4 to 6 layers. The outer layer or two is composed of partially differentiated phloem elements, either sieve cells or frequently phloem parenchyma. The innermost layer adjacent to the last tracheids matured the previous season consists in part of partially differentiated xylem parenchyma strands. When growth is resumed these differentiate into the terminal xylem parenchyma that is a characteristic feature of the wood of Douglas-fir. Thus the xylem parenchyma strands here result from the transverse divisions of xylem mother cells at the end of a growing season, but the resultant parenchyma cells do not mature till growth is resumed the following year. There is a higher percentage of terminal xylem parenchyma in young stems than in older ones.

All the remaining cells can be considered as cambium and no distinction was made between an initiating layer and xylem or phloem mother cells. In all cells the radial walls are thickened and show numerous primary pit fields. The fusiform initials have a radial dimension of from 4 to 6μ in the dormant condition. The length and tangential dimensions vary with the age of the tree as Bailey (1920) described for pine. In Douglas-fir the larger fusiform initials increase in length from an average of about 800μ in a one-year-old tree to approximately 4500μ in a 200-year-old tree. The tangential diameter increases from about 14 to 40μ. The ray initials are 20 to 25μ in height and slightly exceed the fusiform initials in radial and tangential dimensions.

In the Corvallis area, the cambium resumes activity during the middle of March but divisions are infrequent at this time. The first divisions occur in the mother cells nearest the mature xylem. The rate of cell division is rapid during April, May and June. During this period an actively growing tree may have a cambium zone of 15 to 20 layers of cells, any of which may undergo periclinal division (Fig. 1). The rate of cell division decreases during July and, in slowly growing suppressed trees, mitosis may cease during the latter half of the month. In rapidly growing trees, however, mitosis continues into August and rarely into early September. As Bannan (1955) and others have indicated, the periclinal divisions during the period of rapid growth occur mostly in the xylem mother cells. This, in part at least, accounts for the fact that there is so much more xylem produced than phloem. During any one season, in Douglas-fir there

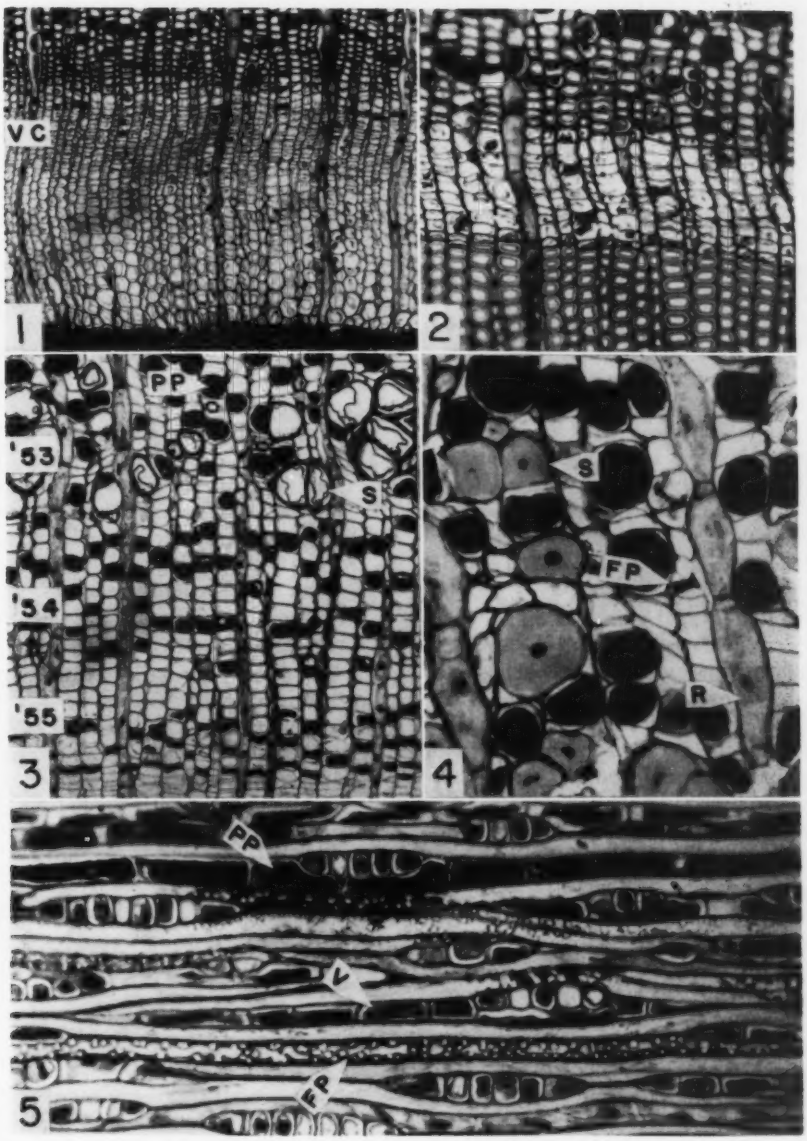


FIGURE 1. *Cambium and new growth of an 18-year-old tree, collected April 23.* FIGURE 2. *Cambium just after mitosis has ceased in 150-year-old tree.* FIGURE 3. *Portion of cambium and three increments of phloem; collected June 29.* FIGURE 4. *Phloem that is 10 years old.* FIGURE 5. *Tangential section of phloem near cambium in an 8-year-old tree. FP, fusiform parenchyma cell; PP, phloem parenchyma strand; R, procumbent ray cell; S. sclereid; V, vertical albuminous parenchyma; VC, vascular cambium. Figures 4, 5, × 200; others, × 100.*

may be over 100 tracheids produced in each tier as compared with only 10 to 12 phloem elements. In slowly growing trees the numbers are much lower but the ratio is about the same.

Differentiation lags considerably behind cell division, especially in a rapidly growing tree. While mitosis is initiated in March and is progressing rapidly in April, the first tracheids of the new growth usually do not develop evident secondary walls until late April or early May (Fig. 1). Differentiation of secondary walls then progresses rapidly. For instance, in a 15-year-old tree with wide growth layers, on May 24 there were about 40 mature tracheids in each tier, 20 to 25 tracheids with walls partly thickened but still retaining protoplasm, and 20 to 25 cells with no evidence of secondary walls. Only 2 to 3 sieve cells of each tier were matured at this time.

When mitosis ceases the cambial zone of thin-walled cells is usually 8 to 10 cells wide (Fig. 2). Only a few of the inner cells continue to differentiate and the growth of the xylem is essentially completed. The outer cells continue to differentiate through September or early October until the dormant cambium of 4 to 6 cells is established. Some of the last elements produced are phloem parenchyma cells on one side of the cambium and xylem parenchyma cells on the other.

Secondary Phloem

The vertical secondary phloem elements in Douglas-fir consist of sieve cells and three types of parenchyma cells. Since each sieve cell is derived from a fusiform initial, and there is little apical or intrusive growth during differentiation, the length varies with the age of the tree. In trees 25 to 35 years old, the sieve cells vary mostly around 3000μ but range from 1000μ to over 4000μ in older trees. The sieve areas on the radial walls are usually in a single vertical row but may be crowded. They vary greatly in size and in number of pores present. Larger sieve cells have sieve areas 15 to 20μ in diameter, with 12 to 18 or more pores. The cell walls are thick and, as in other members of the Abietineae, true secondary walls that are anisotropic are present. Callose deposits that form over the sieve areas in functioning sieve cells will be discussed in later paragraphs.

Parenchyma in the newly formed secondary phloem consists of three types of cells that differ in structure, in physiology as indicated by cell content, and also with regard to changes that occur as the cells become older. The most abundant type of parenchyma is the typical phloem parenchyma strand that results from transverse divisions of a phloem mother cell (Figs. 3, 5, 12). In slowly growing trees there may be only one band produced toward the end of the growing season but in rapidly growing trees usually two bands are produced, one early and the other late in the season. Tangential bands are not evident in some trees, even next to the cambium, and phloem parenchyma strands are dispersed throughout each annual increment. This is more common in young trees.

The parenchyma cells in each strand are rectangular in longitudinal section except for the end cells which are tapered. The cells are rectangular or square in cross section near the cambium, but gradually become rounded and enlarge (Fig. 3). Tanniniferous and resinous materials accumulate in these cells very near the cambium, sometimes before the transverse divisions that produce the strand are completed. Transverse divisions are completed in July or August in the parenchyma strands produced toward the end of the growing season. Some of these cells may not enlarge and accumulate tannins and resins until the following year.

The second type of parenchyma cell found in the phloem of Douglas-fir is known as fusiform phloem parenchyma. This type is derived directly from phloem mother cells without the occurrence of transverse divisions. Thus each cell is approximately the length of the initial from which it was derived. Fusiform phloem parenchyma is much more abundant in the

secondary phloem of young trees, and constitutes only a small percentage of the phloem parenchyma in older trees. These cells differ from the typical phloem parenchyma strands in that most of them accumulate a clear, resinous material, little or none of the granular tanniniferous materials, and numerous cubical crystals soon appear embedded in the resinous material (Fig. 5). After the crystals appear the fusiform parenchyma cells collapse radially and become crushed between adjacent cells. However, they do not disintegrate for several years and traces of the resin and crystals may be found in older phloem (Fig. 4).

There are occasional derivatives that are intermediate between phloem parenchyma strands and fusiform parenchyma cells. These result when only a few transverse divisions of the phloem mother cells occur. Thus there are some short cells and some long ones in each strand. In general, there is a correlation between cell length and type of cell content developed. The short cells tend to accumulate tannins and resins as they do in a typical phloem parenchyma strand, and the longer cells usually accumulate clear resins and crystals. Also, the former persist and expand while the latter tend to collapse early.

The third type of vertical phloem parenchyma differs from the others in that tannins, resins or crystals are not accumulated (Fig. 5). Small amounts of starch may be present in these cells during the dormant period. Chrysler (1913) described the occurrence of this type of cell in other members of the Abietineae. Both Chrysler and Barghoorn (1940) indicated that these cells are associated with the erect or albuminous cells that occur along the margins of the phloem rays in some conifers. Physiologically, the parenchyma cells under discussion are essentially vertical albuminous cells although Strasburger (1891) indicated that such do not occur in Douglas-fir. Well developed sieve areas are present in the walls of sieve cells that contact these parenchyma cells (Fig. 6). Callus plugs develop over these areas (Fig. 7) and the cells collapse as the adjacent sieve cells cease to function.

The vertical albuminous cells may occur as single strands that resemble phloem parenchyma strands. They differ in that resins and tannins are not accumulated, adjacent sieve cells develop sieve areas in conjunction with pits in the albuminous cell, and the albuminous cells collapse after the sieve cells cease to function. More frequently the albuminous cells occur as radial plates of cells (Fig. 6) with the greatest longitudinal dimension in the older phloem at the point of origin of the plate. The initials that originate these plates of cells are produced only toward the phloem side of the cambium since corresponding plates of short parenchyma cells do not occur in the xylem except where the shortened initials become converted to ray initials. Bannan (1951, 1953) has described in detail the origin of such plates in *Thuja* and *Chamaecyparis* by subdivision of fusiform initials. As segments of the initials shorten by subsequent asymetric divisions, some lose their capacity to divide while others continue to shorten and become converted into ray initials. In Douglas-fir, these ray initials may initiate new rays or may add tiers of erect cells to newly formed rays that consist of procumbent ray parenchyma.

The cells that initiate a radial plate may originate in at least two different ways. An initial may become subdivided transversely into a strand of relatively short cells. Mitotic activity in this tier of cells then dwindles and each succeeding strand becomes shorter. The radial plate may be rapidly reduced to one cell which matures and the plate is terminated (Fig. 8). If cambial divisions continue, a new ray is initiated or the cells of the radial plate become transformed into erect cells of a ray as described by Chrysler (1913) and Barghoorn (1940). In some cases, 1- or 2-celled rays consisting only of erect cells are produced (Fig. 9). The initial may also be longitudinally divided unequally after which the smaller cell initiates a radial plate.

Vertical albuminous cells may also result

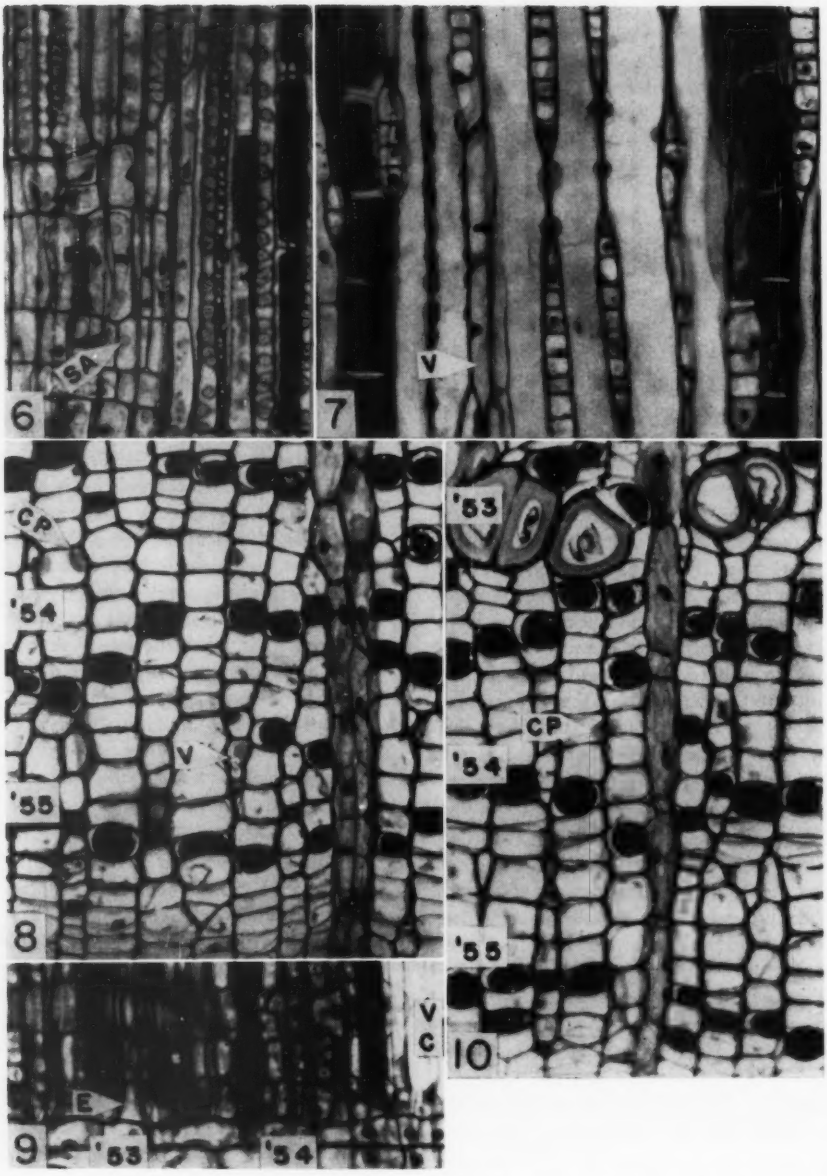


FIGURE 6. *Radial section of radial plate in second-season phloem.* FIGURE 7. *Tangential section of second-season phloem to show callus plugs.* FIGURES 8, 10. *Cross sections of inner phloem; collected August 2.* FIGURE 9. *Radial section of second-season phloem; collected May 10. The small ray above consists of erect cells only. CP, callus plug; E, erect cell; SA, sieve area; V, radial plate of vertical albuminous cells. Figure 6, ×100; others, × 200.*

when a phloem mother cell is divided by a single transverse division. One of the resultant cells then develops as a short sieve cell while the other becomes subdivided to produce a short strand of vertical albuminous cells. These usually persist as an isolated strand.

In addition to the radial plates that originate independently of rays, unequal divisions of initials may produce elongate vertical parenchyma cells that connect the top margin of one ray with the bottom margin of another ray directly above. The initials that produce these cells become subdivided, separate vertically, and gradually produce typical erect cells of the rays involved.

Thus, regardless of origin, the characteristics of the vertical albuminous cells and erect cells are similar. Both accumulate some starch during dormancy, but no resins or tannins. Most of the cells develop primary pit fields in juxtaposition with well developed sieve areas in adjacent sieve cells. Callose deposits develop over the sieve areas (Fig. 7) and both types of cells lose their cytoplasm and collapse shortly after the adjacent sieve cells cease to function. The vertical albuminous cells here bear some resemblance in both origin and behavior to the parenchyma cells in *Calycanthaceae* that are ontogenetically related to sieve tube elements (Cheadle and Esau, 1958).

The radial plates of vertical albuminous cells are relatively more abundant in young stems than in older ones. This may be correlated with the fact that most of the uniseriate rays in young stems are only a few cells high and frequently lack erect cells. In older stems, the rays become higher and erect cells are almost continuous along the margins. The larger rays range in height up to 15 or 20 cells. These eventually become subdivided into two rays by the intrusion of a fusiform initial. The erect cells have denser cytoplasm and larger nuclei that stain more heavily with hematoxylin than in the procumbent cells. The procumbent cells adjacent to the cambium contain little starch during the height of cambial activity. Starch does accumulate late in the growing season and is abundant during the winter. The erect cells contain small amounts of starch only during dormancy.

There are no fusiform rays in young stems. In older stems, the ray initials giving rise to fusiform rays with resin canals show no intercellular spaces in tangential sections of the cambium. The fusiform ray in the cambium is uniseriate at top and bottom, then biseriate, and seldom more than 4 cells wide at the widest point. Only 4 to 6 initials that originate the epithelial cells of the canal are evident in tangential section. A single intercellular space develops in the center of this group of cells very early in the differentiation of the phloem. As the canal increases in diameter, the epithelial cells undergo only an occasional cell division during the first few years after their formation by the cambium. The epithelial cells do not contain tannins and their cytoplasm and nuclei are denser than in other cells of the fusiform ray.

Effects of Age

Some of the elements of the secondary phloem survive for only a year or two, but other elements persist and function for several to many years. The clearest indication of this is seen in trees that are 25 to 35 years old in which the superficial cork cambium is still functional. Some of the phloem parenchyma strands and the procumbent parenchyma cells of both uniseriate and fusiform rays in the oldest phloem are still functional. After a deep cork cambium is differentiated in the secondary phloem, the age of the oldest functional elements is difficult to determine because the annual increments are very indistinct. Strasburger (1891) considered that in pine the phloem parenchyma remained functional for 12 to 25 years. In Douglas-fir the parenchyma strands and rays might live for at least 35 years and probably longer in old, slowly growing trees. Some of the elements perform secondary functions associated with increasing age of the phloem.

The annual increments of secondary phloem are not easy to determine in most conifers. There are some differences in the

diameters of spring and summer sieve cells but these may be obscured by pressures resulting from the expansion of phloem parenchyma strands. The time of formation and number of tangential bands of phloem parenchyma produced each season may be useful in determining increments (Huber, 1949; Holdheide, 1951) but in many trees the bands are not regular. In *Picea* the annual increments are clearly marked by a row of collapsed cells at the boundary between yearly increments (Huber, 1939). In *Chamaecyparis* and *Thuja* (Bannan, 1955) the first fibers of each season's growth have thicker walls than the later fibers.

In this study, the relative diameters of sieve cells, the distribution of the tangential bands of phloem parenchyma, the collapse of erect and vertical albuminous cells, and the appearance and dissolution of callus plugs have all been used to determine annual increments. To avoid confusion, actual dates by years will be used frequently to indicate annual increments. Since the material on which this study is based was collected during 1955, any new growth is indicated for that year.

Most of the literature indicates or implies that in the conifers the sieve cells function for only one growing season. Huber (1939, 1949) indicates that in *Picea, Abies* and *Pinus* the sieve cells also function through most of the second season. This is true also for Douglas-fir. To determine this, only those samples were considered in which the tangential bands of parenchyma were distinct and differences between spring and summer sieve cells were evident. While a sharp distinction between annual increments cannot always be made, the approximate number of phloem elements produced could be determined. The cambium produces only 4 to 8 elements in each tier in slowly growing trees but rapidly growing trees may develop 10 to 12 elements.

The cycle of callus plug formation is considered to be particularly significant in determining the length of time the sieve cells are functional. Here we are concerned primarily with the large deposits that have been considered as definitive callus plugs since these can be seen easily without special staining. All evidence indicates that such plugs develop only in functional sieve cells. Through the early part of the growing season, all or nearly all callus plugs that were present during the winter are dissolved. New plugs develop, usually starting during June, and appear first in the sieve cells of the phloem formed during 1954 (Figs. 8, 10). The deposits are scattered at first and develop apparently at random. That is, one sieve cell may not show any evident deposits (Fig. 7) except for the small collars of callose in each pore. Also, callus plugs may appear over sieve areas in contact with erect cells or vertical albuminous cells before appearing over sieve areas connecting with adjacent sieve cells.

The large plugs then appear more or less progressively in the sieve cells of the 1954 increment and then in the first cells of the new growth of 1955. Callus plugs were not observed in this new growth until after the middle of July. The plugs in both increments persist into the dormant season. When the plugs are dissolved early the next season (assumed to be 1956, in this case) the sieve cells produced in 1954 would be nonfunctional. The callose is lost more slowly from these cells. The sieve cells of 1955 would develop a second deposit of callose during 1956. Thus the first plugs formed in a sieve cell should not be considered as definitive callus but as provisional or dormancy callus (Esau, 1950). The callus plugs of the second year, however are definitive.

The development of the erect cells of the rays offers additional evidence that the sieve cells function through much of the second growing season after they are produced. Radial sections show that they retain nuclei and cytoplasm well into the phloem of the previous year (Fig. 9). They then lose the cell contents and collapse as plugs develop in adjacent sieve cells.

Some of the sieve cells may become crushed by the expanding phloem parenchyma strands toward the end of the season after they were produced. Many of

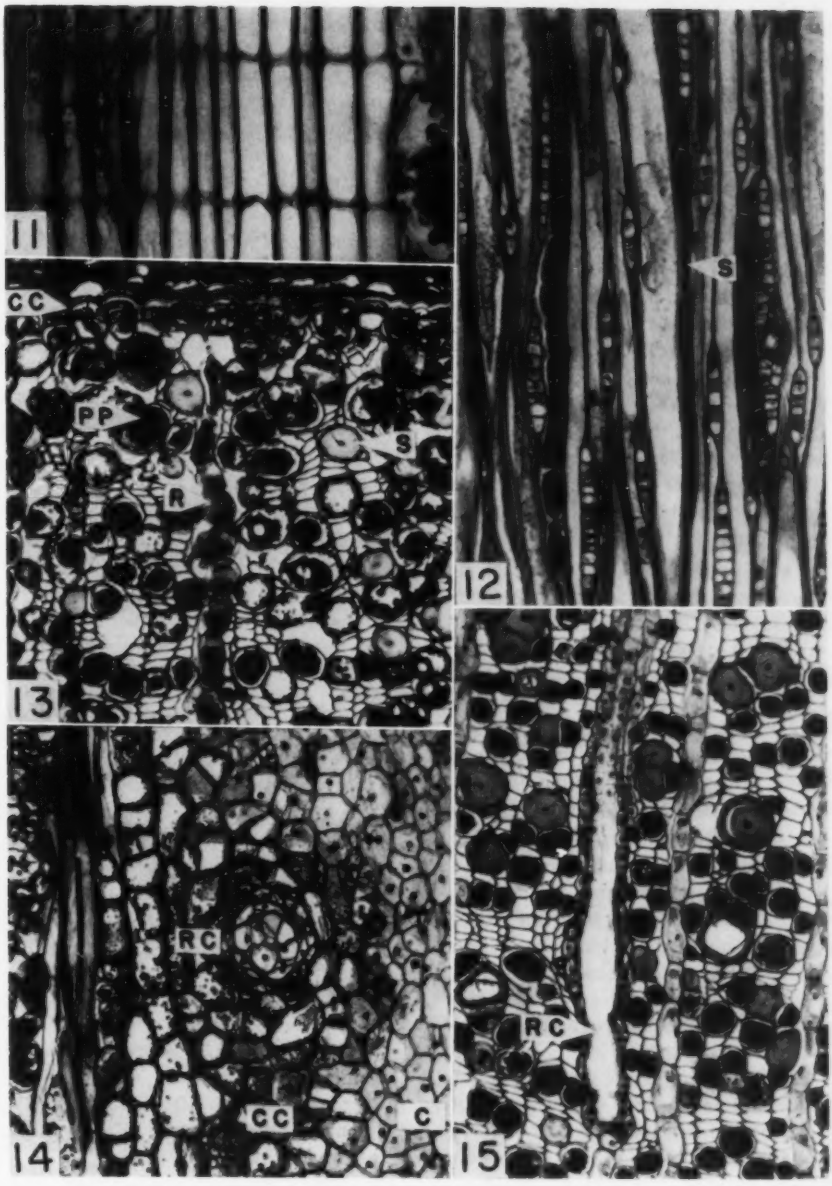


FIGURE 11. *Trabeculae in sieve cells.* FIGURE 12. *Tangential section of third-season phloem to show origin of sclereid by expansion of a parenchyma cell originally located at point of label S.* FIGURE 13. *Cross section of old phloem and deep cork cambium.* FIGURE 14. *Tangential section of old phloem (left), cork cambium, and cork.* FIGURE 15. *Cross section of phloem 4 to 7 years old. C, cork; CC, cork cambium; S, sclereid; RC, resin canal.*

them, however, retain their approximate size and shape for many years except where they are crushed locally by developing sclereids (Figs. 3, 4, 13, 15).

Trabeculae in phloem seldom have been described although Sanio (1873) indicated that such structures extend through xylem, cambium and phloem. Trabeculae were observed in only one tier of cells where they traversed both sieve cells (Fig. 11) and phloem parenchyma cells.

Changes with increasing age of the fusiform phloem parenchyma cells have already been mentioned. These cells collapse in their radial dimension shortly after they become filled with resins and crystals. The collapsed cells and their contents may persist for years in the older phloem (Fig. 4). They never recover and they contribute nothing to the development of the old secondary phloem.

The radial plates and other vertical albuminous cells lose their cell contents toward the end of the season after the one in which they were produced, and after callus plugs develop in adjacent sieve cells (Figs. 6, 7). The relatively few vertical albuminous cells that are not connected by pits to functional sieve areas (Fig. 7) may persist for a longer period of time but they do not accumulate resins or tannins and do not expand in the older phloem.

The phloem parenchyma strands, however, undergo several changes. From the time they are first differentiated they tend to increase in diameter each year, and to accumulate more tannins, resins and starch. Also, during the second year after they are differentiated (in phloem produced in 1953 in our material), some of the cells in the phloem parenchyma strands lose much of the resins and tannins, increase greatly in size, and differentiate as sclereids (Figs. 3, 10 ,12). These cells begin to enlarge about the middle of May. At first the initiation of new sclereids is restricted to the one annual increment but later some older phloem parenchyma cells differentiate additional sclereids (Fig. 15). Thus the number of sclereids in older phloem may gradually be increased for years, probably for as long as living phloem parenchyma strands are present.

The growth of the developing sclereid may be very irregular so that branched and forked cells are not uncommon. Most sclereids, however, expand to one side of the phloem parenchyma strand and grow only vertically (Fig. 12) by intrusive growth to produce pointed, fiber-like cells that are 50 to 100μ in diameter and up to 4000μ in length, though most are somewhat shorter. They occur singly or in groups of 2 to 6. The groups seen in cross section are usually the result of sclereids originating at different levels but growing past each other as they elongate.

The deposition of the lamellae composing the thick secondary wall of a sclereid progresses very slowly. Usually by the middle of July the wall is only about one-third completed (Fig. 10) and the final layers are not deposited till August or September. Resinous materials are present in the small cell lumen but no evidence of nuclei or cytoplasm was detected in mature sclereids.

These sclereids in Douglas-fir have been referred to as phloem fibers by Kiefer and Kurth (1953) and others, but are not to be confused with the true phloem fibers that occur in *Cupressaceae*. These sclereids also differ in structure and origin from those found in the cortex and pith of young stems (Sterling, 1947a) and those found in the cortex of the hypocotyl of seedlings (Smith, 1958). The secondary phloem of *Abies* develops similar sclereids from phloem parenchyma cells (Holdheide, 1951) though they are more irregular in shape.

The cells of the phloem parenchyma strands that do not develop sclereids continue to increase in diameter until they are essentially isodiametric. This ultimately crushes the sieve cells completely after they are 20 to 35 years old (Fig. 13). As the stem increases in diameter the cells proliferate slowly so that in older phloem there are almost continuous tangential sheets of parenchyma cells. These will be interrupted by sclereids and by rays of both types.

The rays also contribute to these sheets of parenchyma. The uniseriate rays become distorted in the outer phloem due to collapse of sieve cells, development of sclereids, and the tensions and compressions resulting from secondary growth. The erect cells have collapsed late in their second year of development. The procumbent ray parenchyma cells gradually increase in diameter and separate somewhat from each other. They accumulate large amounts of starch but usually not much tannins or resins until they are 15 to 20 years old (Figs. 10, 13, 15). They do not proliferate as do the cells of the phloem parenchyma strands. The cells of the fusiform rays tend to accumulate tannins and resins earlier than those of the uniseriate rays. The epithelial cells proliferate in older phloem and finally fill the resin canal with thin-walled parenchyma cells (Fig. 14).

Thus secondary phloem that is 20 to 35 years old consists of parenchyma cells that are derived largely from phloem parenchyma strands, partly from procumbent ray parenchyma cells, and in lesser amounts from proliferated epithelial cells. Interspersed are the crushed sieve cells, almost obliterated fusiform parenchyma cells, and sclereids. Usually no traces of the vertical albuminous cells or erect cells can be found. This area is now capable of differentiating a deep cork cambium (Figs. 13, 14). Based on the material at hand, the first deep cork cambium appears to result from the progressive differentiation of a cambium downward across the cortex from the superficial cork cambium, and hence into the secondary phloem.

This study is not concerned with the activities of the cork cambiums but a few points should be noted. The cork cambium appears to be activated much later in the growing season than the vascular cambium. Samples from some trees showed that the cork cambium may be inactive in some parts of the tree but very active in other portions. When the deep cork cambium is active, it usually produces more cork in a season than does a superficial cork cambium. A deep cork cambium usually functions for only a few years before it is killed by cork produced deeper in the phloem. In old, slowly growing trees a deep cambium may remain active in a given area for 15 years or more. Occasionally, especially in older trees, the cork cambium produces woody cork cells that develop thick, lignified walls with simple pits. The woody cork here represents modified phellum and is not derived from the phelloderm as suggested by Chang (1954). The cambium produces little or no phelloderm. When the cork cambium is dormant or dividing at a slow rate, the cells are filled with resins and tannins. These become much reduced in an actively dividing cambium (Fig. 14).

Summary

In the area near Corvallis, Oregon, the vascular cambium of Douglas-fir resumes activity in March and divisions are most rapid in April, May and June. Activity continues into August, rarely into September, in rapidly growing trees but ceases in July in slowly growing trees. The amount of secondary phloem produced in each tier varies from as few as four elements in suppressed trees, to approximately twelve when growth is rapid. The vertical elements consist of sieve cells, phloem parenchyma strands, fusiform phloem parenchyma, and vertical albuminous cells that may or may not be associated with erect cells of the rays. The sieve cells function for parts of two growing seasons. The fusiform parenchyma cells collapse soon after they are differentiated. The erect cells and vertical albuminous cells collapse during the season after they are differentiated when associated sieve cells cease to function. During the third season some of the cells in phloem parenchyma strands differentiate into large sclereids. The remainder of the phloem parenchyma strands, procumbent ray parenchyma cells, and epithelial cells survive for 20 to 35 years after which they may differentiate a deep cork cambium. Trabeculae were observed that traversed both sieve cells and phloem parenchyma cells.

Literature Cited

ABBE, L. B., and A. S. CRAFTS. 1939. Phloem of white pine and other coniferous species. Bot. Gaz. 100: 695-722.

ALCORN, S. M., and P. A. ARK. 1953. Softening of paraffin-embedded plant tissues. Stain Tech. 28: 55-56.

ALLEN, G. S. 1946. Embryogeny and development of the apical meristems of *Pseudotsuga*. I. Fertilization and early embryogeny. Amer. J. Bot. 33: 666-677.

———. 1947a. Embryogeny and the development of the apical meristems of *Pseudotsuga*. II. Late embryogeny. *Pseudotsuga*. II. Late embryogeny. Amer. J. Bot. 34: 73-80.

———. 1947b. Embryogeny and the development of the apical meristems of *Pseudotsuga*. III. Development of the apical meristems. Amer. J. Bot. 34: 204-211.

BAILEY, I. W. 1920. The cambium and its derivative tissues. III. A reconnaissance of cytological phenomena in the cambium. Amer. J. Bot. 7: 417-434.

BANNAN, M. W. 1951. The reduction of fusiform cambial cells in *Chamaecyparis* and *Thuja*. Can. J. Bot. 29: 57-67.

———. 1953. Further observations on the reduction of fusiform cambial cells in *Thuja occidentalis* L. Can. J. Bot. 31: 63-74.

———. 1955. The vascular cambium and radial growth in *Thuja occidentalis* L. Can. J. Bot. 33: 113-138.

BARGHOORN, E. S., JR. 1940. Origin and development of the uniseriate ray in the Coniferae. Torrey Bot. Club Bull. 67: 303-328.

CHANG, YING-PE. 1954. Bark structure of North American Conifers. U. S. Dept. Agric. Tech. Bull. No. 1095.

CHEADLE, V. I., and K. ESAU. 1958. Secondary phloem of Calycanthaceae. Univ. Cal. Publ. Bot. 29: 397-510.

CHRYSLER, M. A. 1913. The origin of the erect cells in the phloem of the Abietineae. Bot. Gaz. 56: 36-50.

CRAFTS, A. S. 1943. Vascular differentiation in the shoot apices of ten coniferous species. Amer. J. Bot. 30: 382-393.

ESAU, K. 1950. Development and structure of the phloem tissue. II. Bot. Review 16: 67-114.

HOLDHEIDE, W. 1951. Anatomie mitteleuropäischer Gehölzrinden. Handbuch der Mikroskopie in der Technik V (1): 193-367.

HUBER, B. 1939. Das Siebröhrensystem unserer Bäume und seine jahreszeitlichen Veränderungen. Jahrb. wiss. Bot. 88: 176-242.

———. 1949. Zur Phylogenie des Jahrringbaues der Rinde. Svensk. Bot. Tidskr. 43: 376-382.

ISENBERG, I. H. 1943. The anatomy of redwood bark. Madroño 7: 85-91.

JOHANSEN, D. A. 1940. Plant microtechnique. McGraw-Hill, New York.

KIEFER, H. J., and E. F. KURTH. 1953. The chemical composition of the bast fibers of Douglas-fir bark. Tappi 36: 14-19.

SANIO, K. 1873. Anatomie der gemeinen Kiefer (*Pinus silvestris* L.). Jahrb. wiss. Botan. 9: 50-126.

SHIMAKURA, M. 1936a. On the sclerenchyma of bast in conifers. Bot. Mag. Tokyo 50: 206-213.

———. 1936b. On the expansion of bast cells in conifers. Bot. Mag. Tokyo 50: 318-323.

SMITH, F. H. 1958. Anatomical development of the hypocotyl of Douglas-fir. For. Sci. 4: 61-70.

STERLING, C. 1946. Organization of the shoot of *Pseudotsuga taxifolia* (Lamb.) Britt. I. Structure of the shoot apex. Amer. J. Bot. 33: 742-750.

———. 1947a. Sclereid formation in the shoot of *Pseudotsuga taxifolia*. Amer. J. Bot. 34: 45-52.

———. 1947b. Organization of the shoot of *Pseudotsuga taxifolia* (Lamb.) Britt. II. Vascularization. Amer. J. Bot. 34: 272-280.

STRASBURGER, E. 1891. Ueber den Bau und die Verrichtungen der Leitungsbahnen in den Pflanzen. Hist. Beiträge Bd. 3. Gustav Fischer, Jena.

Influence of the Seed Coat on Germination, Water Absorption, and Oxygen Uptake of Eastern White Pine Seed

BY
THEODORE T. KOZLOWSKI
ARTHUR C. GENTILE

GERMINATION of white pine seed can be hastened by several pregermination treatments such as soaking in sulfuric acid or water, cold storage in wet sand or vermiculite (stratification), or removal of the seed coat (Stone, 1957a). Since pine seeds germinate more promptly when divested of their seed coats it has been postulated that true embryo dormancy often does not occur, or at least is not a serious deterrent to germination in many lots of seed. The present work was undertaken to study the effect of the seed coat on germination, water uptake, and oxygen uptake of the seed of eastern white pine (*Pinus strobus* L.).

Materials and Methods

Germination of intact and punctured seeds. Intact and punctured seeds were planted in vermiculite in greenhouse flats and the course of their germination observed over a 52-day period under greenhouse temperatures which varied from 95° F in the daytime to 68° F at night. Each of three flats was divided into two sections by a board running lengthwise. In each flat, 200 intact seeds were planted in one section and 200 seeds with punctured seed coats in the other. Flats were watered daily. Each punctured seed had the tip of the seed coat broken with a razor blade before planting, care being taken not to injure the seed contents. The six groups of 200 seeds each were randomly selected in advance of assignment to treatments or to location in the flats. The seeds used in this experiment (from central Wisconsin) proved to be low in viability.

Moisture content of intact and punctured seeds during germination. Since the seed lot used in the previous experiment had a low germination percentage, another lot of seed, obtained from the Adirondack Mountains of New York State, was used for the present and all subsequent experiments. All comparisons made between various experiments pertain to this same seed source. Punctured and intact white pine seeds were grown in greenhouse flats containing a sandy loam soil under the conditions previously described. The flats were watered daily and duplicate lots of 10 punctured and 10 intact seeds were withdrawn from the flats at 48-hour intervals for determinations of moisture content. Seeds were withdrawn at the same time of day and before the flats were watered. The withdrawn samples were rapidly washed free of soil in a sieve

---

The authors are with the Dept. of Forestry and Wildlife Management, Univ. Wisconsin, Madison and the Dept. of Botany, Univ. Massachusetts, Amherst.

They gratefully acknowledge assistance from Mrs. Sonya Bergquist, Francis Witham and Theodore Peterson in conducting this study. The cooperation of the Wisconsin Cons. Dept. in providing some of the seed used in this study is also acknowledged. Paper published with approval of Director, Wisconsin Agric. Expt. Sta.

and blotted with filter paper before their fresh and dry weights were determined.

Oxygen uptake of germinating seeds. Seeds were sown in greenhouse flats containing a sandy loam soil under the conditions previously described. Each flat was watered daily and, for measurement of oxygen uptake, four lots of 20 seeds each were withdrawn at 48-hour intervals beginning two days after planting. On the days of sampling, care was taken to withdraw seeds at the same time of day just prior to watering the flats. The replicate lots of 20 seeds each were carefully washed in tap water to remove soil particles. Excess moisture was removed with blotting paper before fresh weights were recorded. Oxygen uptake of each sample of 20 seeds in 0.5 ml of tap water was measured at 28° C in a Warburg respirometer. The center well of each vessel contained 0.2 ml 20 percent KOH and a filter paper wick. At the end of two hours the seeds were removed from the vessels and their fresh and dry weights determined. The final measurements were made 24 days after planting when a number of the seeds had germinated.

Oxygen uptake of intact seeds and seeds without seed coats in air. Intact seeds were soaked in distilled water for 24 hours and then randomly divided into two lots. Seed coats and papery membranes were removed from seeds in one of the lots. These seeds were then placed on moist filter paper. As soon as sufficient seeds had their seed coats removed, their rate of oxygen uptake, as well as that of intact seeds, was determined. Seeds were susended in 1.0 ml, 0.01 M phosphate buffer, pH 6.9 in Warburg vessels. The center well of each vessel contained 0.2 ml of 20 percent KOH and a filter paper wick. Oxygen uptake was measured at 30° C. Twenty seeds were used per vessel and three vessels for each of the two treatments. At the conclusion of the manometric determinations the seed coats and papery membranes of the experimental intact seeds were removed, and the moisture contents of each of the experimental lots were determined.

Oxygen uptake of intact seeds in air and in a high oxygen atmosphere. Intact seeds were soaked for 24 hours in distilled water. Their respiration rates were then determined for 90 minutes in normal air and in air containing a high oxygen concentration. Seeds were randomly divided into two lots. Oxygen uptake of one lot was determined in air while that of the second lot was determined in a commercial gas mixture of 80 percent oxygen and 20 percent nitrogen. The vessels containing the second lot were gassed for 10 minutes with the high-oxygen gas mixture prior to the manometric determinations of oxygen uptake. Oxygen uptake was determined for three separate lots of 20 seeds each, for each of the two treatments.

Oxygen uptake of seeds without seed coats in air and in a high oxygen atmosphere. Seeds were soaked in distilled water for 24 hours. After removal of the seed coats and papery membranes surrounding the seeds the seeds were randomly divided into two lots. Oxygen uptake of one lot was measured in air and that of the other in a commercial gas mixture containing 80 percent oxygen and 20 percent nitrogen. Oxygen uptake was determined for three separate lots of 20 seeds for each of the two treatments.

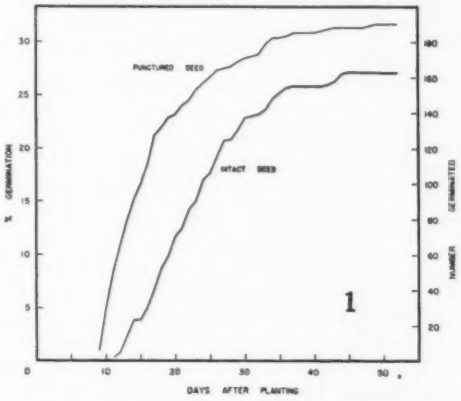
Experimental Results

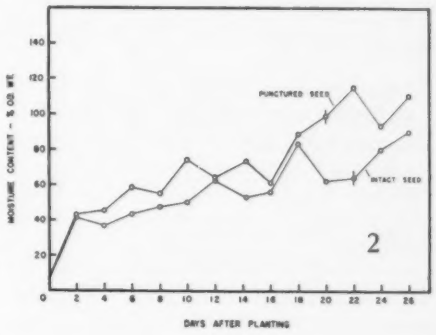
Germination of intact and punctured seeds. The course of germination of intact and punctured seeds is given over a 52-day period in Figure 1. Germination began earlier and was more regular in the punctured lot than in the intact seeds. In fact more than 50 percent of the eventual germination of the punctured lot occurred within a 5-day period, beginning 9 days after planting. In contrast, germination began later and extended over a longer period of time in the intact seeds. The seeds used in this experiment were of rather low viability and only slightly over 30 percent germinated over a 52-day period. Nevertheless, the experiment showed that puncturing the seed coat promoted an early burst of germination. The pattern was con-

sistent and, within each of the 3 flats, total eventual germination percentage was greater in the lot with punctured seeds.

Moisture contents of intact and punctured seeds during germination. Moisture contents of intact and punctured seeds are given over a 26-day period in Figure 2. Water uptake was rapid in both groups during the first 2 days. After this phase, water uptake of both lots continued at a greatly reduced rate. Seeds with punctured seed coats had higher moisture contents than intact seeds in all 13 determinations. However, the differences on some days were small. There was some indication of a greater difference in moisture contents between the two groups beginning at about the time when seed coats burst. Stanley (1958) found a clear three-phase pattern of water uptake in germinating seeds of sugar pine (*Pinus lambertiana* Dougl.). The rapid initial water uptake apparently results from combined osmotic and imbibitional forces of living and dead tissues. After this initial phase the live tissues continue to absorb water at a reduced rate, presumably because of conversion of osmotically inactive to osmotically active substances (Stone 1957a). When the seeds germinate more rapid water uptake follows.

Oxygen uptake of germinating seeds. The course of oxygen uptake over a 24-day period in eastern white pine seeds germinated in greenhouse flats is shown in Figure 3. Under the conditions of the experiment, oxygen uptake appeared to follow three phases: a rapid uptake at 2 days after planting, followed by a decrease and then





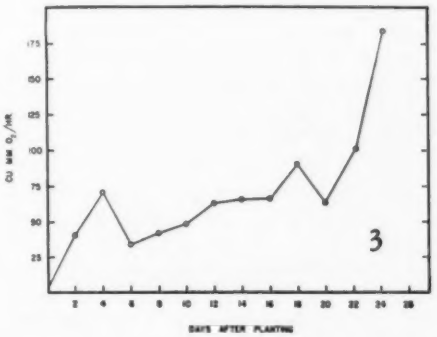


FIGURE 1. *Germination of intact and punctured seeds of eastern white pine.* FIGURE 2. *Moisture content of intact and punctured seeds during germination. Vertical lines on points indicate time when bursting of seedcoats was first observed in each group.* FIGURE 3. *Respiratory capacity of germinating seeds. Seeds were planted in greenhouse flats in soil and samples withdrawn at two day intervals for measurements of oxygen uptake. Data are for 20 seeds at each sampling date.*

a slowly increasing rate until 20 days after planting, and finally a rapid increase. This rapid increase is presumably largely due to the very high rate of the individual seeds whose seed coats were broken, rather than to a large increase in the rate for seeds with unbroken seed coats. In general, the pattern of oxygen uptake was similar to that of water uptake. However, the rate of oxygen uptake after seeds burst increased much more rapidly than the rate of water uptake.

Oxygen uptake of seeds with and without seed coats in air. Figure 4 shows the rate of oxygen uptake of intact seeds and seeds without seed coats in air. Removal of the seed coats markedly increased oxygen uptake, and in fact approximately doubled it. Although there were no significant differences in moisture content between the two groups of seeds at the conclusion of the manometric determinations there were large differences in oxygen uptake of the two groups (Fig. 4).

Oxygen uptake of intact seeds in air and in a high oxygen atmosphere. Respiration data for intact seeds in air and in an atmosphere containing 80 percent oxygen and 20 percent nitrogen are given in Figure 5. Oxygen consumption was essentially linear. Each straight line is fitted to mean values derived from 20 respiring seeds in each of three Warburg vessels. A greatly increased oxygen uptake by seeds in the high oxygen atmosphere is apparent. This increase at 90 minutes is in excess of 50 percent over that of seeds in air.

Oxygen uptake of seeds without seed coats in air and in a high oxygen atmosphere. The results of a time course study on oxygen uptake of seeds without seed coats in air and in a mixture of 80 percent oxygen and 20 percent nitrogen are given in Figure 6. Removal of the seed coat materially increased oxygen uptake over that of the intact seeds in air (Fig. 4). Oxygen uptake of the seeds without seed coats was also increased by replacing air as the gas phase with an 80 percent O_2-20 percent N_2 mixture. It should be noted, however, that this increase was not as marked as the increase in oxygen uptake of intact seeds in a high oxygen atmosphere.

Discussion

The seed coat was shown to be a barrier to germination and to intake of oxygen and water by the seed. Puncturing the seed coat, without injuring the embryo, caused germination to occur more rapidly than it did in intact seeds. This treatment may have induced biochemical changes which necessarily precede germination.

The rate of oxygen uptake by eastern white pine seeds can be increased greatly by surrounding intact seeds with a high oxygen atmosphere. Oxygen uptake can also be accelerated in air by divesting seeds of seed coats and the papery membranes surrounding the seeds. Both treatments increase the partial pressure of oxygen around the embryo which, in the intact seed in air, may be sufficiently low to interfere with certain oxidative reactions necessary for utilization of material accumulated in the seed during stratification such as the intermediates, "I," postulated by Stone (1958). According to Toole *et al.* (1956) the energy requirement for germination onset is met by increased respiration. Thus germination appears to be linked to a threshold of respiratory activity after water is imbibed.

According to Vegis (1956) the real cause of a resting condition is a temperature which is too high for growth of young, recently formed cells which are enclosed by structures limiting oxygen diffusion. Vegis concluded that restricted oxygen access at high temperatures causes reduction in aerobic respiration and activates anaerobic processes. When these changes take place oxidative breakdown of intermediates fails to keep up with their formation and lipids accumulate. Vegis believes that the limiting effect of temperature on growth is basically connected with the accumulation of such lipids as well as growth inhibitors.

Although oxygen uptake and water uptake patterns were somewhat similar under the conditions of the present experiments it

seems doubtful that impeded water uptake in intact seeds was the limiting factor in control of germination. When water uptake of intact and punctured seeds was studied, large differences were not apparent between the two groups until seeds began to burst. These average differences probably were the result of large amounts of water uptake in a few seeds whose seed coats were broken. Since more seeds had germinated in the punctured groups after 22 days, it was not surprising to find a higher average moisture content in this group. The rate of oxygen uptake of seeds in air is markedly increased by removal of their seed coats and papery membranes surrounding the seeds (Fig. 4).

If the seeds without seed coats had taken up more water in the Warburg vessels during the manometric determinations, it would be difficult to rule out increased hydration as a major factor in controlling internal conditions conducive to early germination. Despite large differences in oxygen uptake of intact seeds and seeds without seed coats, there were no apparent differences in the moisture contents of the two groups during the determinations of oxygen uptake. These observations point up the severe oxygen limitation to internal seed tissues imposed by the presence of seed coats, and they deemphasize moisture uptake as normally critical. This condition was also stressed by Stone (1958) in his studies on germination of Jeffrey pine seeds. He found that at 25° C water uptake was closely correlated with germination, but this relationship did not represent a cause and effect. When the temperature was lowered to 5° C water uptake began immediately but germination did not begin for at least 12 weeks.

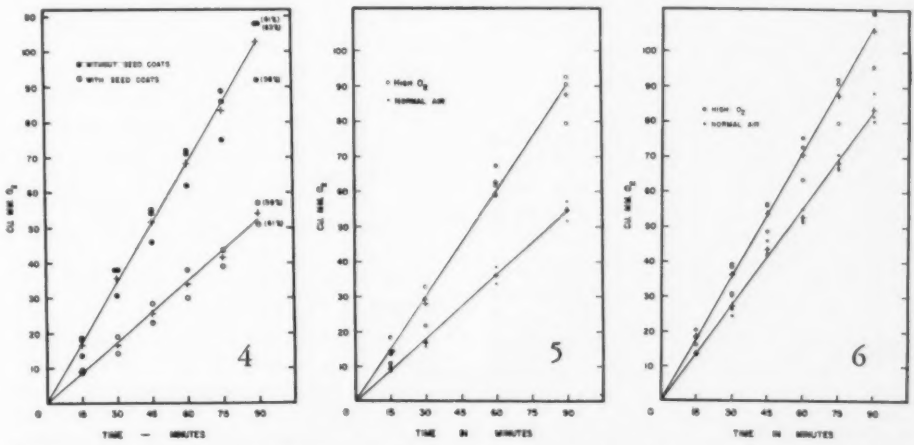


FIGURE 4. *Oxygen uptake of intact seeds and seeds without seed coats in air. The lines are fitted to average values (indicated by +) for each group. Data from three Warburg vessels (20 seeds per vessel) are plotted for the seed without seed coats, and from two vessels for the intact seed. Moisture contents (percent oven dry wt.) of seeds at end of the manometric determinations are given in parentheses.* FIGURE 5. *Oxygen uptake of intact seeds in air and in a mixture of 80 percent oxygen-20 percent nitrogen. Lines are fitted to average values (indicated by +) for each group. Data from three Warburg vessels, each containing 20 seeds, are plotted for each group.* FIGURE 6. *Oxygen uptake of seeds without seed coats in air and in a mixture of 80 percent oxygen-20 percent nitrogen. The lines are fitted to average values (indicated by +) for each group. Data from three Warburg vessels, each containing 20 seeds, are plotted for each group.*

In another experiment Stone (1958) soaked seeds of Jeffrey pine for 48 hours and then put them in sealed test tubes in incubators at 5° C, 15° C and 25° C for 3 months. At the end of that time only the seeds held at 5° C for 3 months germinated successfully. He concluded that all the water uptake necessary for germination occurred during the first 48 hours. Thereafter internal chemical changes were necessary for germination.

In another study, Stone (1957a) found greater water uptake in seeds without seed coats than in intact seeds, but the intact seeds failed to germinate even after the lag in water uptake was overcome. From these various observations he concluded that water uptake alone did not limit germination. Toole *et al.* (1956) cite evidence that gas exchange is limited by seed coats of several species of grasses. Water uptake, however, does not appear to be significantly impeded by seed coats in these species. The results of the present study on seeds of eastern white pine support conclusions of the aforementioned investigators.

Limitation of oxygen uptake by seed coats is characteristic of seeds of a variety of plants (Brown, 1940; Thornton, 1953; Toole *et al.*, 1956; Stone, 1957a). Physical barriers to oxygen diffusion also occur rather generally in tissues other than seeds. For example, bud scales impede oxygen diffusion (Pollock, 1953; Kozlowski and Gentile, 1958). Oxygen tensions between the outer atmosphere and internal tissues of fruits and stems also vary (MacDougal and Working, 1933; Kidd, 1935; Goodwin and Goddard, 1940). The potential respiratory capacity of many internal plant tissues commonly is not realized because of such oxygen barriers.

This study does not indicate differences, if any, in accumulation of inhibitors in seeds with and without seed coats. Further work is needed along such lines. Also, these experiments do not distinguish between internal changes caused by increasing oxygen availability and those caused by stratification. There is some evidence that the effects of stratification and seed coat removal on germination are not identical (Stone, 1957b) and further experimentation is needed to characterize the specific internal changes brought about by both of these treatments. As shown by Stanley (1958), however, increased rates of oxygen uptake occur in stratified seeds before they do in unstratified seeds. Stanley found an upsurge of oxygen uptake in unstratified sugar pine seeds after 60 hours, while in stratified seeds the upsurge occurred after 4 to 24 hours.

Summary

The effect of the seed coat on oxygen uptake, water uptake and germination of eastern white pine (*Pinus strobus* L.) seed was studied.

Germination of eastern white pine seeds with punctured seed coats began earlier and was more rapid that that of intact seeds. Moisture uptake patterns of germinating eastern white pine seeds were rather similar to those of oxygen uptake. Water uptake was greater in punctured seeds than in intact seeds during the course of germination. Oxygen uptake of germinating eastern white pine seed followed three phases: a short period of rapid uptake, a longer period of decreased uptake until seed coats were broken, and then a greatly accelerated rate.

Removal of seed coats markedly accelerated oxygen uptake of seeds in air. Exposure of intact seeds to high oxygen concentration markedly accelerated their rate of oxygen uptake. Removal of seed coat, followed by exposure of seeds to high oxygen concentration, resulted in even greater rates of oxygen uptake than did removal of seed coats alone or exposure to high oxygen concentration. The seed coats of eastern white pine seed appear to be a serious barrier to oxygen diffusion to internal tissues. This barrier seems to be an important factor in preventing early germination of unstratified seed.

Literature Cited

Brown, R. 1940. An experimental study of the permeability to gases of the seed

coat membranes of Cucurbita pepo. Ann. Bot. 4: 379-395.

GOODWIN, R. H. and D. R. GODDARD. 1940. The oxygen consumption of isolated woody tissues. Amer. J. Bot. 27: 234-237.

KIDD, F. L. 1935. Respiration of fruits. Nature 135: 327-330.

KOZLOWSKI, T. T. and A. C. GENTILE. 1958. Respiration of white pine buds in relation to oxygen availability and moisture content. For. Sci. 4: 147-152.

MACDOUGAL, D. T. and E. B. WORKING. 1933. The pneumatic system of plants, especially trees. Carnegie Inst. Wash. Publ. 441: 1-87.

POLLOCK, B. M. 1953. The respiration of Acer buds in relation to the inception and termination of the winter rest. Physiol. Plantarum 6: 47-64.

STANLEY, R. G. 1958. Gross respiratory and water uptake patterns in germinating sugar pine seed. Physiol. Plantarum 11: 503-515.

STONE, E. C. 1957a. Embryo dormancy of P. Jeffreyi Murr. as affected by temperature, water uptake, stratification, and seed coat. Plant Physiol. 32: 93-99.

———— 1957b. Embryo dormancy and embryo vigor of sugar pine as affected by length of storage and storage temperatures. For Sci. 3:357-371.

———— 1958. The seed dormancy mechanism in pine. In The Physiology of Forest Trees. K. V. Thimann, Ed. Ronald Press, New York, N. Y.

THORNTON, N. C. 1953. Dormancy. In Growth and Differentiation in Plants. W. E. Loomis, Ed. The Iowa State College Press, Ames, Iowa.

TOOLE, E. H., S. B. HENDRICKS, H. A. BORTHWICK, and V. K. TOOLE. 1956. Physiology of seed germination. Ann. Rev. Plant Physiol. 7: 299-324.

VEGIS, A. 1956. Formation of the resting condition in plants. Experientia 12: 94-99.

Forest Fire: Control and Use

By Kenneth P. Davis. New York: McGraw-Hill Book Company, 1959. 584 pp., illus. $12.

Review by John J. Keetch
Forest Service, U. S. Department of Agriculture

Because it is the first book-length treatment of the subject, this publication becomes at once a milepost in forest fire control. The author, very wisely, has emphasized approaches, and principles. Thus, though treatment centers on the United States, with recognition of similar problems in Canada, the basic principles should apply anywhere in the world where wild land fire control is attempted. Professor Davis has written a very valuable book.

The style is clear and flowing and has a vitality that could only come from experience on the fireline. The author is exceptionally well qualified for handling this subject. His U. S. Forest Service career included duty from fire guard to fire boss on large national forest fires, a number of years in research, and a period in Washington as Chief of the Division of Forest Management Research. From Dean of the School of Forestry at Montana State University he went to the University of Michigan, where he is now Professor of Forest Management and Chairman of the Department of Forestry, School of Natural Resources.

The book is divided into 3 parts and 20 chapters, including 10 pages of index and 22 pages of bibliography. Chapter outlines are conveniently arranged in the table of contents. An introductory statement precedes each of the three parts of the book, explaining the purpose of the material in that section. A preliminary statement in Chapter 1, by providing general background prepares the reader for the professional treatment which follows. Summaries in most chapters of what has gone before and brief accounts of what is to come help orient the reader.

Part 1 (7 chapters) explain fire as a natural phenomenon in the forest. This is a very logical starting point because an awareness of what a fire can do is basic to an appreciation of the need for organized fire control, and a potent stimulus to learn how to go about it. Included are latest concepts and most recent knowledge of fire effects, combustion, behavior, fuels, and fire danger rating. Chapters on combustion of forest fuels and forest fire behavior were written by George M. Bryam, Physicist, Southeastern Forest Experiment Station, Forest Service, whose work has had a profound effect on forest fire research. He here explains his "fire system model" and the important new "unifying concept" in the understanding of fire behavior. W. R. Krumm, Fire Weather Meteorologist, U. S. Weather Bureau, explains the part played by temperature, air moisture, atmospheric stability, large scale subsidence, and other factors in the start and spread of fires. A comparative analysis of the principal fire danger rating systems in the United States and Canada is a unique feature of Part 1 and is particularly significant in view of the current emphasis on developing a unified fire danger system in the United States.

Part 2 deals admirably with the methods of controlling forest fires, presenting one phase of the job at a time, from prevention, detection, use of tools and line building, through organization problems and control of large fires. Features of special interest to the reviewer were (1) the section on aerial detection and operation of an airground system, (2) the illustrated sections on use of hand tools and power equipment in control line building, and (3) the special treatment of water and chemicals in fire suppression. The section on air-borne tankers is especially timely.

Part 2 concludes with an unusual presentation of "The Practice of Fire Control." The essence is conveyed by means of four case examples "to bring the smell of smoke into the story." In starting to read this section, the reviewer was prepared to skim over quickly the eyewitness accounts of actions on going fires. But after beginning, it was difficult to stop. The writing is vivid and altogether realistic. It appears to be a very effective way of integrating the principles discussed in previous chapters and of explaining their application in field situations.

In Part 3, attention is directed to fire control objectives, and the use of fire as a tool in land management. In one chapter, special consideration is given to an analysis of the factors that should be considered in determining how much should be spent on fire control. Two others deal interestingly with the use of fire in forest land management and the application of prescribed burning.

A thorough and fair appraisal of different points of view pervades the book. The text is amplified by more than 100 illustrations and 26 tables. Intended as a college text, it should, in addition, be extremely useful as a basic teaching guide in fire training schools anywhere, and should have tremendous interest to all who are concerned about fire in the forest.

FOREST SCIENCE OWNERSHIP STATEMENT

Statement of the ownership, management, etc., required by the Acts of Congress, March 3, 1933, and July 2, 1946, of FOREST SCIENCE, published quarterly at Baltimore, Md., for December, 1959.

DISTRICT OF COLUMBIA

Before me, a Notary Public, Washington, D. C., personally appeared L. Audrey Warren, who having been duly sworn according to law, deposes and says that she is the Business Manager of FOREST SCIENCE and that the following is, to the best of her knowledge and belief, a true statement of the ownership, management, etc., of the aforesaid publication for the date shown in the above caption, required by the Act of March 3, 1933, embodied in section 537, Postal Laws and Regulations, to wit:

1. That the names and address of the publisher, editor, and business manager are: publisher, Society of American Foresters, Mills Building, Washington 6, D. C.; editor, Stephen H. Spurr, School of Natural Resources, University of Michigan, Ann Arbor, Michigan; business manager, Miss L. Audrey Warren, Mills Building, Washington 6, D. C.

2. That the owner is the Society of American Foresters, Mills Building, Washington 6, D. C. Stockholders owning 1 per cent or more of total amount of stock are: None.

3. That the known bondholders, mortgagees, and other security holders owning or holding 1 per cent or more of total amount of bonds, mortgages or other securities are: None.

4. That the two paragraphs next above, giving the names of the owners, stockholders and security holders, if any, contain not only the list of stockholders and security holders as they appear upon the books of the company but also, in cases where the stockholders or security holders appear upon the books of the company as trustee or in any fiduciary relation, the names of the person or corporation for whom the trustee is acting, is given; also that the said two paragraphs contain statements embracing affiant's full knowledge and belief as to the circumstances and conditions under which stockholders and security holders who do not appear upon the books of the company as trustees, hold stock and securities in a capacity other than that of a bonafide owner; and this affiant has no reason to believe that any other person, association, or corporation has any interest direct or indirect in the paid stocks, bonds, or other securities than as so stated by her.

L. AUDREY WARREN, *Business Manager*

Sworn to and subscribed before me this 8th day of September, 1959 (seal). Spencer T. Money, Notary Public, Washington, D. C. (My commission expires May 15, 1969.)

Some Sampling Attributes of the Negative Binomial Distribution With Special Reference to Forest Insects

BY
W. E. WATERS
W. R. HENSON

IT IS BECOMING increasingly evident that a proper understanding of the aggregative tendencies of animals is basic to ecological research. Yet the relation of spatial distribution to behavior patterns, population dynamics, and evolutionary trends has not been fully explored. Real understanding of these relationships requires detailed study.

With "contagious" distributions, the initial problem to be faced is the confusion of biological components with purely statistical ones. These components must be distinguished if any reasonable interpretation is to be made of the dispersal pattern and frequency distribution of an organism in spatial units of its natural habitat.

Usually, fitting observed field counts of insects (and other organisms, both plant and animal) to theoretical frequency distributions has been done (1) to derive a transformation that will normalize the data for valid estimates of sampling and experimental errors and the tests of significance and other statistical procedures related thereto, or (2) to determine in a general way the random or non-random nature of the distribution of individuals in a population. Analyses of the latter sort have led in turn to speculations as to the reproductive and dispersive processes involved or, alternatively, to possible effects of local heterogeneity in the environment (Goodall, 1952).

To these objectives should now be added that of obtaining a valid and meaningful measure of aggregation. Some real progress in this direction has been made by plant ecologists (Skellam, 1952; Moore, 1954; Clark and Evans, 1954; Thompson, 1956). However, with animals in general and insects in particular, the complexities engendered by mobility and different life stages with unique behavior patterns have thus far dampened enthusiasm for this approach.

Moreover, interpretation of frequency distribution data *per se* has certain limita-

---

This paper is a portion of a dissertation submitted to Yale University by the senior author as partial requirement for the Ph.D. degree.

The authors are, respectively, Entomologist, Northeastern Forest Experiment Station, Forest Service, U. S. Department of Agriculture, New Haven, Conn., and Assistant Professor, School of Forestry, Yale University, New Haven, Conn.

Appreciation is expressed to M. L. Prebble, Chief, Division of Forest Biology, Science Service, Canadian Department of Agriculture, for permission to include the *Eriophyes* field data in the analyses presented here; to George M. Furnival, School of Forestry, Yale University, for his counsel on certain statistical aspects of the problem; and to F. B. Lewis, Northeastern Forest Experiment Station, U. S. Forest Service, for assistance in the dissection of the loblolly pine tips and identification and counting of the tip moth larvae.

tions that must be recognized. Blithe acceptance of a good agreement of observed data with the calculated values of a theoretical series may lead to entirely unwarranted conclusions (Walker, 1942; Skellam, 1952). First, the observed data might satisfactorily fit more than one distribution. Second, the same distribution can arise from several distinct mathematical and biological models. Third, the parameters of most discrete frequency distributions are strongly influenced by the form and size of sampling unit and by population density.

In the present study, first consideration was given to the negative binomial series because of its wide applicability to biological data and the relative ease of computing its parameters. It has been found to describe satisfactorily a variety of counts of different stages of several forest insects (Morris, 1954, 1955; Waters, 1955). Evans (1952), Pielou (1957), and others showed that the size of sampling unit greatly affected the estimated parameters of "contagious" distributions and, in fact, might alter the form of the distribution itself. Hence with the specific insects under study, this factor was investigated first. This paper is limited to that aspect of the problem. The presentation is intended to be mainly descriptive; no mathematical solutions will be evolved, although certain important relationships may now become clearer.

Distribution Patterns in Forest Insect Populations

Proper quantitative data have been obtained for very few forest insects. *Forest insect* is here defined as any species that *feeds* in or on a forest tree during at least one stage of its life cycle. The term generally connotes a species of economic importance. The ranges, life histories, behavior patterns, and spatial distributions are known of a small fraction of the species, diminishing in that order. However, certain relationships involving sampling-unit size, numbers present, and frequency distribution are known from theory and experience; these should be clarified before presenting specific data on them.

Although various discrete or discontinuous frequency distributions have been amply described in statistical and ecological writings, the relation between them is often not made clear. And in many instances a specific distribution has been utilized with no reference to its underlying assumptions and biological significance. The sections immediately following deal briefly with some well-known distributions generally termed "random" and "non-random" or "contagious."

Random Distribution

The normal and Poisson distributions are invariably specified when a random distribution of insect counts is assumed—the normal when counts are "high," the Poisson when counts are "low." The assumption may or may not be justified, although a quick test of fit is often given as justification. As pointed out by certain earlier biometricians (Pearson, 1905; Whitaker, 1914; Student, 1919) and by many later biologists, the theoretical bases of each of these distributions are rarely, if ever, obtained in natural populations. The normal is obviated first because it is a continuous distribution, thus precluding discrete integers, and second because it allows no relation between the variance and mean of the population. The Poisson is generally of doubtful reality because it involves three assumptions rarely met *in toto* (Student, 1919). These assumptions are:

1. Each individual has the same chance of falling into any unit.
2. Each unit has the same chance of an individual falling into it.
3. The presence of one individual in a unit does not in any way affect the chances of another falling into it.

The Poisson, further, is obtained only when the probability of occurrence is very small in relation to the number of insects present. When the probability of occurrence is greater, a binomial (positive or negative) will provide a better, more significant fit to the data.

Under certain circumstances, each of these distributions can be approximated.

However, the cause may be artificial (e.g., enlargement or constriction of sampling-unit size to arbitrary limits) and thus have no biological significance. The total numbers of an abundant species in 1-acre units over a relatively uniform 100-acre stand of host trees might approximate a normal distribution, yet it would be difficult to interpret this in biological terms. On the other hand, total tree counts of first-instar larvae known to have but limited movement from the egg (or egg mass) could conceivably approach a normal distribution, and a reasonable inference would be that no significant inter-tree selection in egg deposition was shown by the adult females. This is not suggested as the most practical way of obtaining information on the inter-tree variation in larval counts or on the egg-laying habits of the insect, but to show that the inferences to be drawn depend on the kind as well as size of sampling unit. The tree in this case is a natural and meaningful unit; the acre is not—at least not for the one count.

As an example in the case of low numbers, counts of the eggs of an insect (even at a high population level) in square-centimeter units of leaf-surface area quite probably would show no significant departure from the Poisson expectation. Here, the probability of finding eggs in any unit has been made very small simply by reducing the size of the sampling unit. The unit, moreover, is an artificial one. However, counts of a needle miner in single needles would undoubtedly fit the Poisson at very low population levels, and, assuming a limit of just one insect per needle, would grade into the positive binomial as the population increased and the probability of a miner being in a needle increased. One step further: the total numbers of this needle miner on branches or branch whorls might approximate the normal distribution at a high population density so long as no selective stratification of the population between branches or whorls occurred. Stark (1952) reported that counts of the lodgepole needle miner on 5-year branch tips from two elevational levels generally containing high populations saisfactorily approximated the normal distribution.

These examples, simplified but nonetheless possible, demonstrate that there is a recognizable relationship between the random distributions themselves involving relative size of sampling unit and population density. Some possible relations of these with non-random series are described in the following sections.

Non-Random Distribution

Departure from randomness is pictured in its simplest form as deviations from the three necessary conditions of the Poisson series given above. Although Condition 1—all individuals having an equal chance of falling into a unit—rarely holds, Student (1919) showed that it was generally unimportant unless the chances of certain individuals falling into a particular unit or group of units was relatively high. In this case the tendency would be toward a positive binomial. Condition 2—equal receptivity, or attractiveness, of all units—is usually not met under natural conditions. This results in a negative binomial form of distribution. Condition 3 is seldom true in natural populations. If the presence of an individual in a unit increases the chances of another occurring there, the negative binomial distribution will result.

Several of the earlier theoretical distributions such as those of Greenwood and Yule (1920) and Pólya (1931), which have been more widely used in other fields of inquiry (e.g., accident proneness, epidemiology) than in ecology, were derived essentially by the consideration of deviations of a specified nature from Conditions 2 and 3. Other distributions based on biological models have been developed more recently—Neyman's (1939) "contagious," the discrete lognormal, and Thomas's (1949) "double Poisson"—but these will not be discussed here. They all relate, however, to Condition 2 and involve different expectations of occurrence in individual units.

Beall and Rescia (1953) presented a generalization of the Neyman series, in

which the terminal type closely matches the negative binomial but is considerably more complex mathematically. Among the few frequency distributions of forest insects analyzed thus far, the distribution of attacks by *Ips pini* adults in lodgepole pine slash was best described by Neyman's distribution (Reid, 1957). The numbers of eggs per curled shoot of the larch sawfly, *Pristiphora erichsonii* (Htg.), were reported by Ives (1955) to follow a modified lognormal distribution.

The interesting empirical approaches of Walker (1942) and Cole (1946) to the problem of assessing aggregation in natural populations should be mentioned briefly, as they indicate more fully the scope of the problem. Walker was concerned with the distribution of eggs of the American bollworm, *Heliothis armigera* Hbn., on corn plants. She constructed a distribution representing the summation of a varying number of component random distributions at each of two times. She developed her hypothesis from a knowledge of the behavioral activities of the egg-laying moths in relation to phenological development of the host plant. The hypothesis was that there existed a continuous change in attractiveness of individual plants to the moth and that this change could be approximated by considering the plant population at any given time to contain a relatively small number of distinct categories of attractiveness, within each of which egg-laying occurred at random. Therefore, probability of egg deposition within each category was assumed to be constant, but different for each category.

An empirically derived "mixed distribution" was suggested also by Fracker and Brischle (1944) with reference to the frequency distribution of *Ribes* in quadrats. Both random and non-random elements were involved in the latter case, however.

Cole (1946) proposed that contagious distributions be considered as a superimposition of independent random distributions of groups of 1,2,3,...n, individuals. Parameters representing the density of single individuals, pairs, singles and pairs, etc., are fitted in turn. Cole found that, applied to populations of a variety of ground fauna, this compound distribution generally fitted the data much better than Neyman's series. However, as many as six parameters were used, compared with two for the Neyman distribution; so it is not surprising that a better fit was obtained. This method of analyzing aggregation is undoubtedly laborious, but it should provide the basis for rather interesting interpretations, particularly in conjunction with others methods of analysis.

"Contagion"—Biological Fact or Sampling Artifact?

A clarification of the term "contagion" is much needed. Feller (1943) clearly distinguished between *true contagion* and *apparent contagion*. The first exists, he states, where the occurrence of an individual in a unit of space or time increases or decreases the chances of others occurring in the same unit; the latter is due solely to heterogeneity in the population. Not too clearly understood, however, is the fact that this heterogeneity may be real, reflecting either a variation in the behavior patterns of the insect, or a lack of uniformity in the microenvironment, or both. On the other hand, it may be imposed by the method of sampling (Feller, 1943; McGuire *et al.*, 1957). When the data are obtained by sampling, undoubtedly all components are involved.

Greenwood and Yule (1920) considered both kinds of "contagion." The mathematical solution of the situation described by true contagion proved too cumbersome for practical use, but the problem of heterogeneity in the form of a compound Poisson distribution was readily solved. The Neyman and Thomas series are perhaps the simplest examples of compound Poisson distributions and apparent contagion. The negative binomial, although developed from the Poisson distribution and closely related to it (Quenouille, 1949), can also arise from a number of other known causes (to be discussed). It can include contagious elements of both kinds, and is more com-

plex in that sense. But because of this the negative binomial permits more valid interpretation of the biological factors involved.

"Contagious" distributions thus involve both biologically significant and strictly artificial components. These must be distinguished if a working knowledge of aggregation and its effects in natural populations is to be obtained.

The Negative Binomial Series

This frequency distribution was early recognized to be of importance in biology (Pearson, 1905; Whitaker, 1914). But only recently have the mathematical complexities involved in estimating its parameters and applying it to ecological data been simplified enough for practical use by quantitatively minded ecologists (Haldane, 1941; Anscombe, 1949, 1950; Bliss and Fisher, 1953). It has proved particularly applicable to insect counts (Anscombe, 1949; Wadley, 1950; Evans, 1953; Bliss and Fisher, 1953; Morris, 1955).

The negative binomial series is characterized by a continuous variation (in time or space) of the expectation of counts in individual units, this expectation varying in a distribution proportional to that of χ^2. It is defined by two parameters, the arithmetic mean m and a positive exponent k, which are theoretically independent but in practice appear rarely so. The distribution is generally expressed by the expansion of

$$(q-p)^{-k} \text{ where } p=\frac{m}{k} \text{ and } q=1+p.$$

The curve derived is unimodal, so that any bimodality in observed counts is charged to random sampling (Anscombe, 1950). With increasing randomness, the variance of the distribution approaches the mean, $p \to 0$, $k \to \infty$, and the Poisson is obtained. With increased aggregation $k \to 0$, and if only the units with insects are included, the logarithmic series results (Fisher *et al.*, 1943). In comparison with the other nonrandom distributions mentioned previously, the negative binomial shows more skewness and a smaller proportion of zero counts for a given mean and variance, except for the discrete lognormal distribution, which is the most highly skewed of those generally tested.

The negative binomial series can arise in at least five different ways (Bliss and Calhoun, 1954):

1. Heterogeneity in the probability of occurrence.
2. True contagion: where the presence of one individual in a unit increases the chance that another will occur there also.
3. Compounding of Poisson and logarithmic distributions: when the number of colonies, or definite groups of individuals, is distributed at random and the number of individuals per colony follows a logarithmic distribution, the number of individuals per unit will form a negative binomial series.
4. Birth-death-immigration process: the growth of a population with constant rates of birth and death per individual and a constant rate of immigration per unit of time leads to a negative binomial distribution for population size.
5. Inverse binomial sampling: if a given proportion of individuals in a population possess a certain character, the number of observations in excess of k that must be taken to obtain just k individuals with the character has a negative binomial distribution with exponent k.

Only models 1, 2, and 3 have been considered in the present investigation.

Effects of Sampling-Unit Size

Complete counts on individual trees were obtained of a gall mite, *Eriophyes* sp., and the Nantucket pine tip moth, *Rhyacionia frustrana* (Comst.). The mite is a cosmopolitan but rather innocuous pest commonly found on the leaves of quaking aspen, *Populus tremuloides* Michx., the host from which these particular data were taken. The tip moth is an economically important pest of natural and planted pines throughout the Atlantic coastal plain. It characteristically infests the buds and new shoots of host trees and is especially abundant on lob-

lolly pine, *Pinus taeda* L., from which species these counts were obtained. The counts of each organism were tabulated according to different sampling units and analyzed in terms of the respective frequency distributions.

Gall Mite Data

These data were collected in connection with a long-term bioclimatic study of poplar insects in the trans-Divide region of the Canadian Rocky Mountains (Henson, 1954). The counts are from 18 trees at Kootenay Crossing, Kootenay National Park, British Columbia. Sample trees were selected in a random manner, felled, and cut into smaller units for careful examination. The trees varied in diameter from 4.6 to 8.9 cm at breast height and from 4.1 to 7.9 m in height.

The total number of leaf galls on each of the 18 trees were recorded. The counts were then tabulated according to five progressively larger sampling units: (1) the individual leaf, (2) the leaf-bunch, (3) two leaf-bunches, (4) five leaf-bunches, and (5) the branch. A thorough analysis of the distribution of foliage on the sample trees at Kootenay Crossing and other locations showed that the number of leaves per

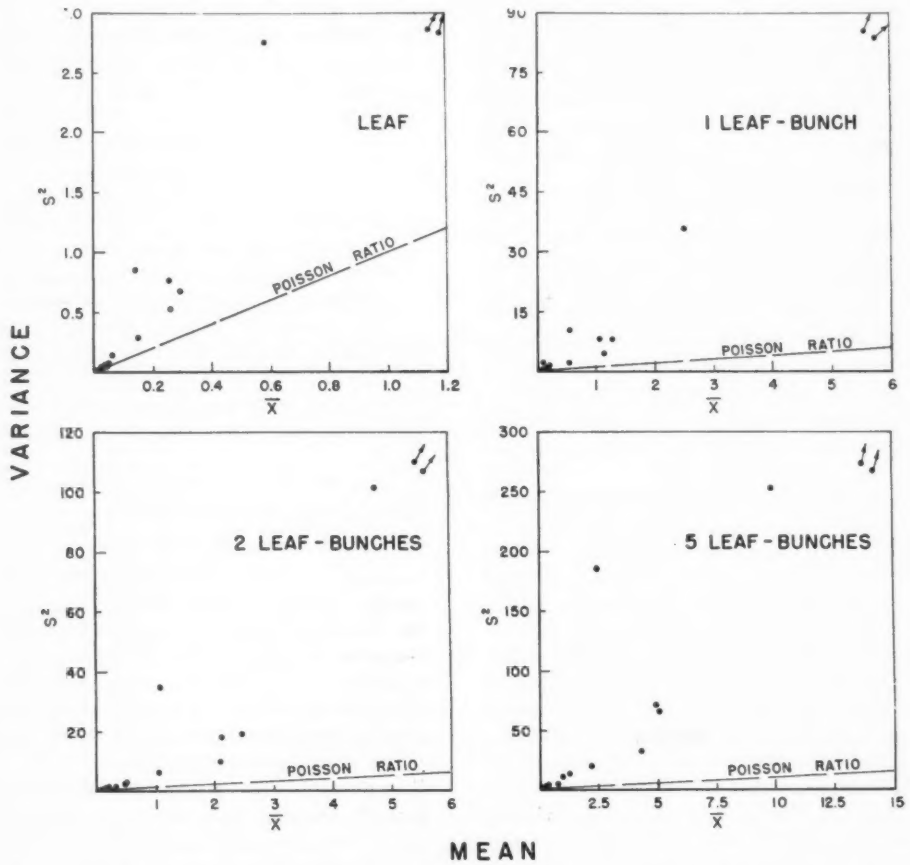


FIGURE 1. *Variance-mean relationships of* Eriophyes *leaf galls on sampling units of quaking aspen.*

bunch was remarkably constant over all crown levels, quadrants, whole trees, and locations (Henson, 1954). The number of leaves per bunch for the Kootenay Crossing trees averaged 4.28. Pitted galls on the leaf surfaces were counted rather than the mites because the galls were very small, and time limitations did not permit the checking of every one for mites present. The observations made, however, indicated that each gall was caused by one mite.

The "over-dispersed" or aggregative nature of the counts on the different sampling units is clearly shown by the variance-mean relationships (Fig. 1). The branch-unit data are not included, but they were of the same pattern as the other unit sizes. The variance/mean ratio of a Poisson distribution is 1, and this relation holds over all population levels. The observed data depart noticeably from this expectation except at very low population levels. This is a frequently observed characteristic of "contagious" distributions. In attempting to identify the true frequency distribution of an organism, therefore, both high and low population levels should be represented. The variance-mean relationships of the *Eriophyes* counts also show a positive curvilinearity. This has appeared in quadrat sampling of many plant and animal populations and has been the basis for a number of indices of dispersion devised by earlier plant and animal ecologists (e.g., Fracker and Brischle, 1944).

The mean number of *Eriophyes* leaf galls per sampling unit and estimates of the negative binomial parameter k for each size of unit are given in Table 1. The estimates of k were obtained by two methods, as indicated: (1) equating the observed proportion of zero counts to the expected proportion (method 2 of Anscombe, 1949), and (2) the regression method of Bliss (cf. Bliss and Calhoun, 1954). In this paper, these will be referred to as Method I and Method II, respectively. For the range of k values and related means found, Method I gave estimates of well over 90 percent efficiency (from efficiency diagram of Anscombe, 1949) for all sampling units. The efficiency of the Method II estimates was not determined.

The calculated k's given in Table 1 are

TABLE 1. Mean number of Eriophyes leaf galls per sampling unit and estimates of the respective k *values.*

Sampling unit	Leaf galls (mean number)	Estimates of k	
		Method I[1]	Method II[2]
Single leaf	0.21±0.01	0.0611±0.0013	0.3578±0.2666
1 leaf-bunch	.88± .04	.0883± .0024	.4034± .2666
2 leaf-bunches	1.65± .08	.1150± .0035	.4972± .3697
5 leaf-bunches	3.78± .26	.1740± .0064	.4830± .3854
Branch	14.23±1.68	.2000± .0119	([3])

[1] k is selected by successive approximation to satisfy $n_0 = N\left(1 + \frac{\bar{x}}{k}\right)^{-k}$ where n_0 = number of 0 counts, N = total number of observations, and $\bar{x}$ = mean count.

[2] Utilizing the mean counts and within-tree variances for individual trees, $k = \frac{\left(\Sigma \bar{x}^2 - \frac{s^2}{N}\right)}{\Sigma (s^2 - \bar{x})}$ where $\bar{x}$ = mean count per tree, s^2 = within-tree variance, and N = number of observations per tree.

[3] There were not enough branches on all trees to permit calculation of this k.

the pooled values for all 18 trees. They appear to become larger as the size of units is increased. This is more striking for Method I values than for those of Method II. This apparent trend is questionable, however, as the overall counts for each of the sampling units show an extremely poor fit with the negative binomial, and the pooled k's thus cannot be considered valid.

The total observed and expected frequencies for the different units are shown in Table 2 with their corresponding χ^2 values. The total χ^2 in each case indicates a probability of less than 0.001 that the observed discrepancies arose solely by chance. The frequencies listed were calculated using the k's estimated by Method I (the fit using the regression estimates of k, Method II, was worse in all cases). Apparently a common or pooled k calculated by Method I can have a deceptively low standard error (Table 1) and still be unusable. The cause of this dilemma is indicated by the very large standard errors of the regression estimates, which are based on individual tree values. These large errors reflect the extreme heterogeneity in the distributions on the individual trees. It appears that the relation between sampling-unit size and the parameter k must be assessed on the basis of individual tree values rather than the average values over all trees.

The calculated k values for the different sampling units on individual trees are given in Table 3. They range from near 0 to ∞ in all sampling-unit series. They are the individual values that were pooled by means of regression to provide estimates of k for the 18 trees as a group. Although no "errors" can be attached to these point values, and thus no tests of the significance of differences between them can be made, it is evident that in general the k values do increase noticeably with the increase in size of sampling unit. For example, the change in k's for Tree 1 (0.130, 0.168, 0.270, and 0.378) is proportionately much greater than the change in pooled k's from 0.3578 to 0.4972.

It is equally evident that the relationship between sampling-unit size and k varies considerably among the trees. A low population tree, Tree 3 (0.0067 mite galls per leaf), retains its Poisson characteristic of $k = \infty$ over all sizes of sampling unit. This might be ascribed simply to the low counts; yet another tree, Tree 17, with an equally low population (0.0065 galls per leaf) shows definite signs of aggregation with respect to k for all of the units. Two trees, 13 and 14, with similar k values for the smallest size of unit show quite different changes in k with increasing size of unit. In this case, the k's for Tree 13 range from 0.054 to 0.084, while those of Tree 14 range from 0.055 to 0.152. The k values for the high-population trees are apparently more stable. For example, the k's for the two highest population trees in the group, Tree 9 ($\bar{x} = 1.6102$ per leaf) and Tree 11 ($\bar{x} = 2.1069$ per leaf), range only from 0.479 to 0.531 and 0.384 to 0.518 respectively. These interactions can be fully interpreted only when the biological facts are known.

In summary then, these data show that *Eriophyes* leaf galls tend to be aggregated on all of the sampling units. However, the degree of aggregation varies considerably between trees, so that it is not possible to derive a valid pooled estimate of k for even so few as 18 trees. The applicability of a single common k to a series of counts of wireworms in soil units was similarly questioned by Bliss and Owen (1958). Moreover, the relationship between sampling-unit size and k is not consistent, although there appears to be a general trend toward larger values of k with increasing size of unit. For *Eriophyes* the tree must be considered as an ecological entity.

Two other points of interest appear in these data. First, the mean number of *Eriophyes* galls per 5 leaf-bunches is not a direct multiple of the mean counts on units of 1 and 2 leaf-bunches (Table 1). This is due possibly to smaller numbers of mites on the leaf-bunches farther back on the branches or fewer leaves per leaf-bunch on

TABLE 2. Total frequencies of Eriophyes leaf galls on different foliage sampling units of aspen—18 trees. Agreement of observed counts with those expected by the negative binomial series tested by χ^2, the expected values based on k *estimated by Method I.*

Mite galls (number)	Single leaf			One leaf-bunch			Two leaf-bunches			Five leaf-bunches			Branch		
	Obs. freq.	Expected freq.	χ^2	Obs. freq.	Expected freq.	χ^2	Obs. freq.	Expected freq.	χ^2	Obs. freq.	Expected freq.	χ^2	Obs. freq.	Expected freq.	χ^2
0	47997	47997.0	0	9933	9933.0	0	4770	4770.0	0	1657	1657.0	0	322	322.0	0
1	2553	2253.0	39.95	1061	797.0	87.45	734	512.8	95.42	436	276.0	92.75	95	63.5	15.63
2	744	921.2	34.09	342	394.1	6.89	247	267.3	1.54	180	155.0	4.03	43	37.6	.78
3	395	487.7	17.62	207	249.3	7.18	158	176.2	1.88	115	107.0	.60	29	27.2	.12
4	273	287.6	.74	143	174.9	5.82	101	128.2	5.70	60	81.2	5.53	30	21.5	3.36
5	160	180.0	2.22	103	129.9	5.57	88	98.7	1.16	45	64.8	6.05	27	17.8	4.76
6	99	117.0	2.77	58	100.1	17.71	40	78.6	18.96	37	53.4	5.04	19	15.2	.95
7	68	78.1	1.31	68	79.1	1.56	41	64.2	8.38	32	45.0	3.76	9	13.3	1.39
8	33	53.1	7.61	53	63.7	1.80	43	53.4	2.03	20	38.6	8.96	8	11.8	1.22
9	39	36.7	.14	34	52.0	6.23	27	45.0	7.20	19	33.5	6.28	12	10.6	.18
10	28	25.6	.23	34	43.0	1.88	29	38.4	2.30	14	29.4	8.07	7	9.6	.70
11	19	18.0	.06	20	35.8	6.97	20	33.0	5.12	18	26.0	2.46	6	8.8	.89
12	25	12.8	11.63	23	30.1	1.68	20	28.6	2.59	14	23.1	3.58	5	8.1	1.19
13	7	9.2	.53	24	25.4	.08	16	24.9	3.18	11	20.7	4.55	6	7.5	.30
14	20	6.6	27.21	18	21.6	.60	14	21.8	2.79	14	18.6	1.14	3	7.0	2.29
15	44[1]	20.4[1]	27.30	12	18.4	2.23	10	19.2	4.41	7	16.8	5.72	3	6.5	1.88
16	—	—	—	8	15.8	3.85	8	16.9	4.69	6	15.2	5.57	6	6.0	0
17	—	—	—	10	13.6	.95	12	15.0	.60	16	13.8	.35	10	5.7	3.24
18	—	—	—	6	11.7	2.78	13	13.3	.01	7	12.6	2.49	2	5.3	2.05
19	—	—	—	6	10.1	1.66	8	11.9	1.28	6	11.5	2.63	115[1]	151.9[1]	8.96
20	—	—	—	5	8.8	1.64	11	10.6	.02	6	10.5	1.93	—	—	—
21	—	—	—	11	7.6	1.52	9	9.5	.03	5	9.6	2.20	—	—	—
22	—	—	—	10	6.6	1.75	12	8.5	1.44	5	8.8	1.64	—	—	—
23	—	—	—	81[1]	48.4[1]	21.96	5	7.7	.95	10	8.1	.36	—	—	—
24	—	—	—	—	—	—	4	6.9	1.22	4	7.4	1.56	—	—	—
25	—	—	—	—	—	—	4	6.2	.78	7	6.8	.01	—	—	—
26	—	—	—	—	—	—	4	5.6	.46	5	6.3	.27	—	—	—
27	—	—	—	—	—	—	81[1]	56.6[1]	10.52	4	5.8	.56	—	—	—
28	—	—	—	—	—	—	—	—	—	4	5.4	.36	—	—	—
29	—	—	—	—	—	—	—	—	—	87[1]	83.1[1]	.18	—	—	—
Total	52504	52504.0	173.41 w/13d.f. $p = <.001$	12270	12270.0	189.76 w/21d.f. $p = <.001$	6529	6529.0	184.66 w/25d.f. $p = <.001$	2851	2851.0	178.63 w/27d.f. $p = <.001$	757	757.0	49.89 w/17d.f. $p = <.001$

[1]This frequency value is the total for the count indicated plus all larger in the distribution. The summation was made at the point where the expected number was 5 or less.

TABLE 3. Regression estimates of the parameter k *for different sampling units on individual trees (Eriophyes data).*

Tree number	k values—Method II			
	Single leaf	1 leaf-bunch	2 leaf-bunches	5 leaf-bunches
1	0.130	0.168	0.270	0.378
2	.138	.151	.242	.403
3	∞	∞	∞	∞
4	.051	.087	.102	.120
5	.027	.029	.034	.034
6	.153	.173	.175	.250
7	.154	.179	.226	.391
8	.258	.377	.512	.676
9	.479	.507	.565	.531
10	.215	.257	.354	.418
11	.384	.430	.561	.518
12	.128	.246	.341	1.432
13	.054	.070	.079	.084
14	.055	.038	.072	.152
15	∞	∞	.407	2.000
16	.195	.217	.244	.180
17	.100	.643	3.600	8.714
18	.102	.122	.233	.309
Regression average	0.3578	0.4034	0.4972	0.4830

the average in the more shaded portions of the branches. This illustrates the need for a full record of the distribution and variability of the sampling unit as well as the organism itself.

Second, in all series there is an excess of 1-counts. This discrepancy between observed and expected "singles" is the major contributor to the χ^2 for all sizes of sampling unit (Table 2). However, the relation between the observed and expected numbers in this category is not constant. The observed/expected ratios increase as the size of unit is increased (at least up to the branch unit). The ratios are given in Table 4. The discrepancy could undoubtedly be corrected and a better fit obtained by an empirically derived distribution. However, this excess of singles probably has a biological origin, and statistical manipulations might serve only to make the interpretation more difficult. The negative binomial series is at least a distribution with known characteristics, and departures from it as a standard can be evaluated closely if sufficient is known of the biology of the mite (or any other organism under study). This knowledge is now lacking.

Nantucket Pine Tip Moth Data

These data were taken in a sampling study aimed at the development of practical survey techniques for the tip moth. The insect counts were made on five sample trees in plots at each of six locations, four in Delaware and two in Maryland. The tree species sampled was loblolly pine, natural growth at one location and planted at the other five. Sample trees ranged up to 2.3 m and averaged 1.2 m in height. The tip moth population density was high at Plots 1 and 2, intermediate at Plots 3 and 4, and low at Plots 5 and 6.

The data were taken when the insects were larvae feeding inside the buds and shoots. The current year's shoots and new buds comprise the entire population universe of this stage of the insect; they will be referred to collectively as "tips." All tips were cut from the sample trees and brought to the Forest Insect Laboratory at New Haven for dissection and counting of larvae present.

The numbers of larvae found were recorded for three sampling units: (1) the tip, (2) the branch whorl, and (3) the tree. The infestation on individual trees varied from 0 to 100 percent of the tips. In fact, 11 of the 30 sample trees were completely free of the insect. Because it

TABLE 4. Ratio of observed to expected 1-counts of Eriophyes leaf galls on different sizes of sampling unit.

Sampling unit	Excess ratio of 1-counts
Single leaf	1.13
1 leaf-bunch	1.33
2 leaf bunches	1.43
5 leaf-bunches	1.58
Branch	1.50

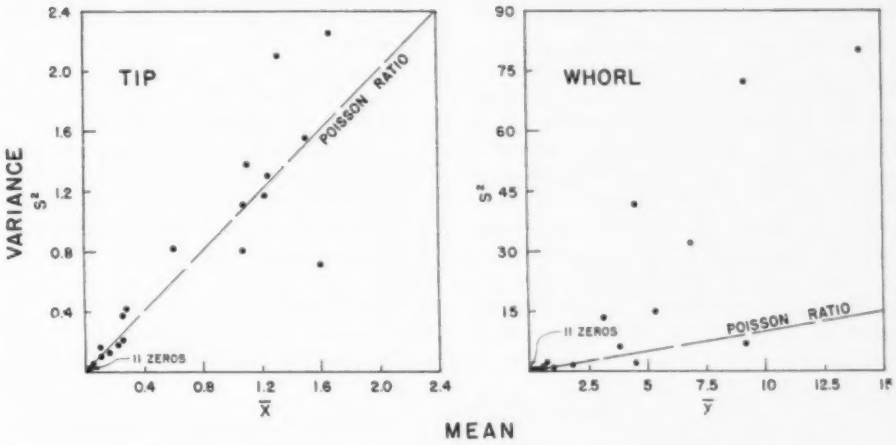


FIGURE 2. *Variance-mean relationships of Nantucket pine tip moth larvae in tips and whorls of loblolly pine.*

was initially assumed that the eggs were deposited on the trees in a random manner (i.e., no selection of certain trees by the moths for egg laying *and* equal receptivity of the trees to egg deposition), the uninfested trees that were picked by chance were included in the analysis. The assumption was verified with respect to the individual plots, as will be shown in a later section.

The variance-mean relations of the tip and whorl counts for each of the 30 trees is shown in Figure 2. The plotted values for the tip unit are well dispersed, but in general they encompass the line of Poisson expectation. This indicates either that the insects are distributed in tips in a random manner or that the range of variation is limited in some way—by the size of sampling unit, say. As will be demonstrated presently, the latter is the case here. The plotted points for the whorl counts depart significantly from Poisson expectation, signifying aggregative tendencies at the whorl level.

The mean number of tip moth larvae and the estimated negative binomial k values for each of the sampling units are given in Table 5. The same two methods of estimating k were used with these data—the approximation of 0's method (Method I) and the regression method (Method II). The efficiency of the estimates by Method I was over 90 percent in all cases; the

TABLE 5. Mean number of Nantucket pine tip moth larvae per sampling unit and estimates of the respective k *values.*

Sampling unit	Mean number of larvae	Estimates of k	
		Method I	Method II
Tip	0.49±0.03	0.449±0.021	13.029±75.932
Whorl	2.36±0.36	.214± .035	2.219± 2.915
Tree	13.13±4.21	.253± .074	([1])

[1]There were not enough sample trees at each location to permit calculation of this k.

efficiency of the regression estimates was not determined.

There is no apparent relation between the estimated k's and the size of unit. The Method I k's are valid estimates; the values estimated by Method II are obviously questionable in view of the magnitude of their standard errors. As the negative binomial form of distribution has apparently been brought about in a somewhat different way for each of the sampling units, the relationship involved will be most clearly shown if each unit is discussed in turn. The sequence will be reversed, however, since the tree is the simplest unit.

The tree. The observed numbers of larvae per tree were as follows:

No. larvae	Frequency	No. larvae	Frequency
0	11	9	1
1	1	16	1
2	2	18	2
3	5	19	1
4	0	32	1
5	1	48	1
6	0	55	2
7	0	99	1
8	0	Total	30

The χ^2 test of fit for a frequency distribution such as this is of doubtful value, so the 3rd moment test described by Anscombe (1950) was used to determine the agreement of this series with the negative binomial. This test avoids distortion due to chance irregularities in the observed frequencies and takes full account of extreme numbers of insects; it is especially suitable when N is too small to permit an effective comparison of observed and expected frequencies (Bliss and Calhoun, 1954). The critical statistic, T, of this test proved to be smaller than its standard error, indicating no significant departure from the negative binomial distribution. This is undoubtedly because six places with different tip moth population levels are represented in the data—resulting in at least three, and perhaps six, more or less distinct expectations of infestation per tree. The compounding of these expectation values produces a distribution of counts per tree that is of negative binomial form.

This, then, is an example of a negative binomial derived simply by the method of sampling—specifically, taking counts on a number of trees at several locations, each of which is relatively homogeneous with respect to size and condition of trees and infestation level but different from the other locations in these respects. This seems to be a more reasonable explanation than the assumption of a uniform expression of "contagion" or aggregation on the 30 trees at locations with different population densities.

The whorl. The total frequencies of tip moth larvae per whorl are shown in Table 6. The agreement between observed and expected is very good, the total χ^2 of 2.78 with 3 degrees of freedom giving a p of 0.43. There is, then, a very definite aggregative distribution of insects by whorls, first indicated by the variance-mean relationship in Figure 2.

A tabulation of the infestation by whorls reveals a consistent difference in the percentage of tips infested. The averages over all 30 trees were as follows: Whorl 1—35 percent, Whorl 2—35 percent, Whorl 3—33 percent, Whorl 4—32 percent, Whorl 5—25 percent, Whorl 6—17 percent, Whorl 7—14 percent, Whorl 8—3 percent, Whorls 9 and over—0. Whorl 1 here is the terminal shoot and bud cluster, Whorl 2 is the first whorl below the terminal, Whorl 3 is the next lower, etc.

Evidently the topmost whorls are most subject to attack by the tip moth, and together (Whorls 1 to 4 in this case) they represent a fairly uniform class of expectation. The lower whorls are characterized by decreasing levels of expectation. Most important, however, is the fact that the relative probabilities of infestation on the successive whorls, or groups of whorls, apparently remain about the same over the range of population densities covered by these data. The frequency distribution that is derived follows the negative binomial very well, and the estimate of k by Method

I is therefore valid. This, then, is an example of the negative binomial arising from a biologically significant effect, aggregative tendencies by the insect.

The large standard error of the k estimated by regression is due primarily to the small number of trees with insects present. The zero counts of the non-infested trees were included in the calculation of k by Method I; by Method II the non-infested trees have no k value and thus contribute nothing to the pooled regression estimate of k.

The tip. The total frequencies of larvae per tip are given in Table 6. The agreement shown is not very good ($p = .09$). This is due in part to the discrepancy between the observed and expected larger numbers of larvae, the observed distribution having fewer and thus being less skewed than the expected negative binomial. The 3rd moment test applied to these data indicated no significant departure from the negative binomial. But the statistic T, the criterion of the test, had a negative sign which suggests that a less skewed distribution would fit the data better.

This approximation of the negative binomial series over all 30 trees implies that the distribution of counts on individual trees must be Poisson-like. The alignment of the variance-mean values in Figure 2 indicates the same tendency. However, the analysis of whorl data gave definite evidence that the insects were not distributed at random on a tree. There was, in fact, a consistent stratification of the population by whorl levels.

The probable explanation of the random-appearing nature of the tip counts is that the numbers are limited by the size of sampling unit. Only 4 tips out of 798 had more than 4 insects in them. If 4 insects is the general limit in the number of larvae that can be contained by any tip, even under heavy population pressure, the larger numbers expected in an aggregated distribution will not occur. A Poisson, binomial, or approximation of the normal distribution will then appear (even though Condition 2 for the Poisson or "random" distribution

TABLE 6. Total frequencies of Nantucket pine tip moth larvae in tips and whorls of loblolly pine—30 trees. Agreement of observed counts with those expected by negative binomial series tested by χ^2, the expected values based on k *estimated by Method I.*

	Tip			Whorl		
Larvae (number)	Observed frequency	Expected frequency	χ^2	Observed frequency	Expected frequency	χ^2
0	572	572.0	0	98	98.0	0
1	122	134.7	1.19	20	19.2	0.03
2	63	51.1	2.79	6	10.7	2.06
3	24	21.8	.22	9	7.3	.43
4	13	9.9	1.01	5	5.3	.02
5	3	4.5	.55	29[1]	26.5[1]	.24
6	1[1]	4.0[1]	2.27	—	—	—
Totals	798	798.0	8.03 w/4 d.f. $p = .09$	167	167.0	2.78 w/3 d.f. $p = .43$

[1]This frequency value is the total for the count indicated plus all larger in the distribution. The summation was made at the point where the expected number was <4.5.

is not fulfilled), depending on the population mean and probability of occurrence. The observed frequency distribution of larvae in the tips (Table 6) does indicate a limitation or truncation of this kind. This situation is slightly more complex than for the other two sampling units.

To summarize, rough agreement with a negative binomial distribution is shown by the counts of larvae in tips over the 30 trees. This is effected by a compounding of random distributions on the individual trees, each with a different mean or expectation. The random nature of the counts on individual trees, however, is due to a limitation in the number of insects that can occur in the sampling unit, a tip.

The k estimated by means of regression (Method II) is worthless in this circumstance. The random or near-random nature of the counts on individual trees results in a wide range of k values, many with negative signs.

Discussion

The two examples considered in this paper are barely indicative of the scope of the problem of evaluating the aggregative distributions of forest insects. First, they represent a very small sample of the kinds of organisms that are of interest to the forest entomologist. And second, the data for each represent essentially just one point in time and space. Moreover, in this paper just one basic problem is analyzed. This problem, the changeable relations between form and size of sampling unit and the negative binomial distribution, is not fully resolved.

Some important relationships are indicated by the analyses of the gall mite and tip moth frequency data and these appear to be interpretable. It is clear that each organism is unique as far as the interactions involved are concerned. The conclusions as to aggregative tendencies based on the data of one sampling unit do not necessarily apply to all spatial units inhabited by the insect. Hence, the use of more than one sampling unit will generally permit a more comprehensive interpretation of the situation.

It is strongly suggested that in ecological studies of forest insects in which the factor of aggregation is involved the raw data be taken, recorded, and analyzed on the basis of two or more sampling units. Insofar as possible, these should be natural spatial units, and the areal or volumetric relationships between them should be known.

Summary

1. The frequency distributions of a gall mite, *Eriophyes* sp., on five different sampling units of quaking aspen are analyzed.

2. The frequency distributions of the Nantucket pine tip moth, *Rhyacionia frustrana* (Comst.), on three different sampling units of loblolly pine are similarly analyzed and interpreted.

3. The negative binomial series is suggested as a standard for evaluation of observed spatial distributions of forest insects.

4. For proper evaluation of the nonrandom distribution of forest insects in natural populations, the first problem to arise is the confounding of biologically significant factors and strictly artificial components. Basic to the resolving of this problem is an understanding of the effect of size and form of sampling unit on the analysis and interpretation of frequency distribution data.

5. The difference between *true* and *apparent* contagion is clarified.

6. It is recommended that data be taken on more than one sampling unit in quantitative studies of the spatial distributions of forest insects. Analyses of the frequency distributions on the different units should provide a basis for separating the truly biological components from the purely statistical.

Literature Cited

ANSCOMBE, F. J. 1949. The statistical analysis of insect counts based on the negative binomial distribution. Biometrics 5: 165-173.

———. 1950. Sampling theory of the negative binomial and logarithmic

series distributions. Biometrika 37: 358-382.

BEALL, G., and R. R. RESCIA. 1953. A generalization of Neyman's contagious distributions. Biometrics 9: 354-386.

BLISS, C. I., and D. W. CALHOUN. 1954. An outline of biometry. Yale Co-op. Corp., New Haven. 272 pp.

———— and R. A. FISHER. 1953. Fitting the negative binomial distribution to biological data and note on the efficient fitting of the negative binomial. Biometrics 9: 176-200.

———— and A. R. G. OWEN. 1958. Negative binomial distributions with a common *k*. Biometrika 45: 37-58.

CLARK, P. J., and F. C. EVANS. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35: 445-453.

COLE, L. C. 1946. A theory for analyzing contagiously distributed populations. Ecology 25: 283-303.

EVANS, D. A. 1953. Experimental evidence concerning contagious distributions in ecology. Biometrika 40: 186-211.

EVANS, F. C. 1952. The influence of size of quadrat on the distributional patterns of plant populations. Contrib. Lab. Vert. Biol., Univ. Mich. No. 54. 15 pp.

FELLER, W. 1943. On a general class of "contagious" distributions. Ann. Math. Stat. 14: 389-400.

FISHER, R. A., A. S. CORBETT, and C. B. WILLIAMS. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. J. Anim. Ecol. 12: 42-58.

FRACKER, S. B. and H. A. BRISCHLE. 1944. Measuring the local distribution of Ribes. Ecology 25: 283-303.

GOODALL, D. W. 1952. Quantitative aspects of plant distribution. Biol. Rev. 27: 194-245.

GREENWOOD, M., and G. U. YULE. 1920. An inquiry into the nature of frequency distributions representative of multiple happenings with particular reference to the occurrence of multiple attacks of disease or of repeated accidents. J. Roy. Statis. Soc. 83: 255-279.

HALDANE, J. B. S. 1941. The fitting of binomial distributions. Ann. Eugenics 11: 179-181.

HENSON, W. R. 1954. A sampling system for poplar insects. Canad. J. Zool. 32: 421-433.

IVES, W. G. H. 1955. Estimation of egg populations of the larch sawfly, *Pristiphora erichsonii* (Htg.). Canad. J. Zool. 33: 370-388.

McGUIRE, J. U., T. A. BRINDLEY, and T. A. BANCROFT. 1957. The distribution of European corn borer larvae, *Pyrausta nubilalis* (Hbn.), in field corn. Biometrics 13: 65-78.

MOORE, P. G. 1954. Spacing in plant populations. Ecology 35: 222-227.

MORRIS, R. F. 1954. A sequential sampling technique for spruce budworm egg surveys. Canad. J. Zool. 32: 302-313.

————. 1955. The development of sampling techniques for forest insect defoliators, with particular reference to the spruce budworm. Canad. J. Zool. 33: 225-294.

NEYMAN, J. 1939. On a new class of "contagious" distributions, applicable in entomology and bacteriology. Ann. Math. Stat. 10: 35-57.

PEARSON, K. 1905. Skew variation, a rejoinder. Biometrika 4: 169-212.

PIELOU, E. C. 1957. The effect of quadrat size on the estimation of the parameters of Neyman's and Thomas's distributions. J. Ecol. 45: 31-47.

PÓLYA, G. 1931. Sur quelques points de la théorie des probabilités. Ann. Inst. Henri Poincaré 1: 117-162.

QUENOUILLE, M. H. 1949. A relation between the logarithmic, Poisson, and negative binomial series. Biometrics 5: 162-164.

REID, R. W. 1957. The bark beetle complex associated with lodgepole pine slash in Alberta. Part IV. Distribution, population densities, and effects of several environmental factors. Canad. Ent. 89: 437-447.

SKELLAM, J. G. 1952. Studies in statis-

tical ecology, I. Spatial pattern. Biometrika 39: 346-362.

STARK, R. W. 1952. Sequential sampling of the lodgepole needle miner. For. Chron. 28: 57-60.

STUDENT. 1919. An explanation of deviations from Poisson's law in practice. Biometrika 12: 211-215.

THOMAS, M. 1949. A generalization of Poisson's binomial limit for use in ecology. Biometrika 36: 18-25.

THOMPSON, H. R. 1956. Distribution of distance to nth neighbor in a population of randomly distributed individuals. Ecology 37: 391-394.

WADLEY, F. M. 1950. Notes on the form of distribution of insect and plant populations. Ann. Ent. Soc. Amer. 43: 581-586.

WALKER, M. G. 1942. A mathematical analysis of the distribution in maize of *Heliothis armigera* Hbn. (*obsoleta* F.). Canad. J. Res., D, 20: 235-261.

WATERS, W. E. 1955. Sequential sampling in forest insect surveys. For. Sci. 1: 68-79.

WHITAKER, L. 1914. On the Poisson law of small numbers. Biometrika 10: 36-71.

Apical Meristem Aging and Silviculture

Investigations on Aging of Apical Meristems in Woody Plants and Its Importance in Silviculture. M. Schaffalitzky De Muckadell. Danish Forest Experiment Station Report No. 201, Copenhagen, 1959, 148 pp., illus.

Review by Robert E. Farmer, Jr.
Lower Michigan Pulpwood Research Association

Developmental stages in woody plants have been recognized by foresters for many years. Early consideration of ontogenetic phases in tree species stemmed from an interest in senility and its accompanying silvicultural problems. At present, however, we recognize several separate stages in plant development each with distinguishing physiological or morphological characteristics. In woody plants a marked difference exists between the juvenile and adult stages, and consequently most research activity has been concerned with the delineation of these two phases.

This monograph represents a further effort to clarify differences between the adult and juvenile stages, the existence of which the author assumes to be due to the aging of apical meristems. It is based upon the author's investigations at the Horsholm Arboretum in Copenhagen between 1953 and 1958.

Chapter I is a rather complete and well written review of reported investigations from the 18th century to present. The various manifestations of ontogenesis are dealt with separately, and special emphasis is placed upon the silvicultural aspects of meristematic aging.

In Chapter II the author reports on several experiments designed to further demonstrate characters associated with the juvenile stage of development. The general technique involves grafting scions of low epicormic shoots and adult wood from a single clone on rootstocks of identical origin. A comparison of these grafts under similar environmental conditions then demonstrates the existence of juvenile characteristics. Major studies were carried out with 12 European hardwood species displaying a total of six categories of distinguishing features, including leaf form, fall coloration, growth form, thorniness, rooting ability, and leaf retention. Much attention is given to leaf retention associated with juvenile phases of *Fagus*, *Carpinus*, and *Quercus*. While striking differences between the two phases were exhibited in all categories by the species studied, the number of grafts was limited in some cases and additional tests may well be needed before the results can be universally accepted.

INDEX TO VOLUME 5, FOREST SCIENCE, 1959

Art.—article; rev.—review; art. (rev.)—review of article or book by.
Authors are indicated by capitals.

Absorption rates of 2,4,5-T tagged with carbon-14. art. 128
Ambrosia beetle Trypodendron lineatum (Oliv.). The overwintering of the. art. 81
ANDERSON, RALPH L. art. 356
Apical meristem aging and silviculture. rev. 412
Balsam gall midge in Wisconsin. The biology and ecology of the. art. 193
BARNES, ROBERT L. art. 158
BARRACLOUGH, SOLON L. rev. 191
BECK, EDWIN. art. 128
BENJAMIN, DANIEL M. art. 193
Bias due to edge effect in using the Bitterlich method. art. 370
Biology and ecology of the balsam gall midge in Wisconsin. The. art. 193
Bitterlich method. Bias due to edge effect in using the. art. 370
BROADFOOT, W. M. art. 2
Budworm, spruce. Mortality of rootlets in balsam fir defoliated by the. art. 64
Cambial activity in black cherry. The initiation of. art. 70
Ceanothus leucodermis and soil nitrogen in southern California mountains. art. 275
Certain ecological and phylogenetic aspects of the pattern of water conduction in conifers. art. 259
Changes in woodland vegetation and soils after spraying large amounts of waste water. art. 18
CHAPMAN, J. A. art. 81
Cherry, black. The initiation of cambial activity in. art. 70
CHING, KIM K. art. 74, 246
CHING, TE MAY. art. 74
Columbian timber beetle and associated fungi in white oak. The. art. 114
Comparison of the Gunn-Bellani radiation integrator and the Eppley pyrheliometer. A. art. 234
Comprehensive and economical designs for studies of spacing and thinning. art. 237
DASMANN, RAYMOND F. rev. 222
Data for planning woodland opportunities on West Tennessee farms. rev. 191
DAVIS, KENNETH P. rev. 395
Decay in northern hardwoods following artificial inoculation with some common heartrot fungi. Rate of. art. 223
DECKER, JOHN P. art. 154, art. (rev.) 291
Distribution of organic matter and plant nutrients in a plantation of Scots pine. art. 344
Douglas-fir and bigcone Douglas-fir. Hybridization between. art. 246
Douglas-fir, bigcone. Photoperiodic control of bud development in coulter pine and. art. 138
Douglas-fir pollen and effects of gibberellic acid on its germination. Extracting. art. 74
Douglas-fir seed as affected by light, temperature, and gibberellic acid. Germination of. art. 174
Douglas-fir. The secondary phloem of. art. 377
DUMBROFF, ERWIN. art. 128
Dwarfmistletoe infection. Brooming response of black spruce to. art. 356
Dwarfmistletoe seed on ponderosa pine. Natural emplacement of. art. 365
Economics of American forestry. rev. 355
Effect of available soil moisture and the mycorrhizal association of Virginia pine. The. art. 267
Effect of temperature on pollen ger-

mination of pinus and its bearing on controlled pollination. art. 10
Elytroderma deformans. Perennial infection of ponderosa pine by. art. 182
Eppley pyrheliometer. A comparison of the Gunn-Bellani radiation integrator and the. art. 234
ESLYN, WALLACE E. art. 37
EVANS, T. C. art. 49
Experimental conservation. rev. 222
Extracting Douglas-fir pollen and effects of gibberellic acid on its germination. art. 74
FARMER, JR., ROBERT E. art. (rev.) 412
Forest fire: control and use. rev. 395
Forestry theses accepted by colleges and universities in the United States —supplement January 1956—June 1958, including additions for 1900-1955. art. 293
Forest succession. A system for analysis of. art. 154
FOSTER, RALPH W. art. 279
FOWELLS, HARRY A. art. 95
FRENCH, D. W. art. 255
GENTILE, ARTHUR C. art. 389
GERHOLD, H. D. art. 333
Germination of Douglas-fir seed as affected by light, temperature, and gibberellic acid. art. 174
GIESE, RONALD L. art. 193
GOULD, JR., E. M. art. (rev.) 191
GRAHAM, SAMUEL A. art. 28
GRILLOS, STEVE J. art. 377
GRUSCHOW, G. F. art. 49
HACSKAYLO, EDWARD. art. 267
HAGA, TOSHIRO. art. 370
HAIG, I. T. rev. 137
Heartrot fungi. Rate of decay in northern hardwoods following artificial inoculation with some common. art. 223
HEIBERG, S. O. art. 142
HELLMERS, HENRY. art. 138, 275
HENSON, W. R. art. 397
Host bark characteristics and infection by Hypoxylon pruinatum (Klot.) Cke. art. 255
Hybridization between Douglas-fir and bigcone Douglas-fir. art. 246
Hybridization in the white pines. Species. art. 210
Hypoxylon pruinatum (Klot.) Cke. Host bark characteristics and infection by. art. 255
Influence of potassium fertilizer level on red pine planted at various spacings on a potassium-deficient site. art. 142
Influence of the seed coat on germination, water absorption, and oxygen uptake of eastern white pine seed. art. 389
Initiation of cambial activity in black cherry. The. art. 70
Inorganic nutrition of loblolly pine and Virginia pine with special reference to nitrogen and phosphorus. The. art. 95
In vitro culture of pine roots and the use of pinus serotina roots in metabolic studies. art. 158
KAUFERT, F. H. art. 356
KEETCH, JOHN J. art. (rev.) 395
KELLEHER, JOHN M. art. 275
KINGHORN, J. M. art. 81
KOZLOWSKI, THEODORE T. art. 389
KRAUSS, ROBERT W. art. 95
KRUGMAN, STANLEY L. art. 169
Leuco-anthocyanin distribution in the genus pinus. The. art. 169
LEYTON, L. art. 142
LITTLE, SILAS. art. 18
LOEWENSTEIN, H. art. 142
LULL, HOWARD W. art. 18
MADGWICK, H. A. I. art. 344
MAEZAWA, KANJIRO. art. 370
Maple, red. Relation between site indexes of eastern white pine and. art. 279
MARTY, ROBERT J. art. 269
McCOMB, A. L. art. 234
McWILLIAM, J. R. art. 10
Methods of vegetation study. rev. 364
MONK, CARL D. art. 229
Mortality of rootlets in balsam fir

defoliated by the spruce budworm. art. 64
Mycorrhizal association of Virginia pine. The effect of available soil moisture on the. art. 267
Native pinewoods of Scotland. The. rev. 157
Natural emplacement of dwarfmistletoe seed on ponderosa pine. art. 365
NAYLOR, AUBREY W. art. 158
Norway, private forestry in—a case study in small woodland management and policy.
For. Sci. Monog. 1 (a separate)
Oak, white. The columbian timber beetle and associated fungi in. art. 114
Organic matter and plant nutrients in a plantation of Scots pine. Distribution of. art. 344
OSBORN, KATHERINE H. art. 293
OSHIMA, NAGAYOSHI. art. 255
Overwintering of the Ambrosia beetle Trypodendron lineatum (Oliv.). The. art. 81
OVINGTON, J. D. art. 344
PARKER, JOHNSON. art. 56
Perennial infection of ponderosa pine by Elytroderma deformans. art. 182
PHILLIPS, EDWIN ALLEN. rev. 364
Photoperiodic control of bud development in Coulter pine and bigcone Douglas-fir. art. 138
Physiology of trees. The. rev. 291
Pine, Coulter, and bigcone Douglas-fir. Photoperiodic control of bud development in. art. 138
Pine, eastern white, and red maple. Relation between site indexes of. art. 279
Pine, loblolly and Virginia pine with special reference to nitrogen and phosphorus. The inorganic nutrition of. art. 95
Pine, ponderosa. Perennial infection by Elytroderma deformans. art. 182
Pine, ponderosa. Natural emplacement of dwarfmistletoe seed on. art. 365
Pine, ponderosa. Root regeneration of seedlings lifted at different times of the year. art. 322
Pine, red, planted at various spacings on a potassium-deficient site. Influence of potassium fertilizer level on. art. 142
Pine, Scotch, in relation to microclimatic factors. Seasonal discoloration of. art. 333
Pine, Scots. Distribution of organic matter and plant nutrients in a plantation of. art. 344
Pine seed, eastern white. Influence of the seed coat on germination, water absorption, and oxygen uptake of. art. 389
Pine, slash, stands. The relation of cubic-foot volume growth to stand density in young. art. 49
Pine, Virginia. The effect of available soil moisture on the mycorrhizal association of. art. 267
Pine, white. Predicting weevil-caused volume loss in. art. 269
Pines, white. Species hybridization in the. art. 210
Pinus, genus. The leuco-anthocyanin distribution in the. art. 169
Pinus serotina roots in metabolic studies. In vitro culture of pine roots and the use of. art. 158
Predicting weevil-caused volume loss in white pine. art. 269
Private forestry in Norway—a case study in small woodland management and policy.
For. Sci. Monog. 1 (a separate)
Pollen germination of pinus and its bearing on controlled pollination. Effect of temperature on. art. 10
Potassium fertilizer level on red pine planted at various spacings on a potassium-deficient site. Influence of. art. 142
Radiographical determination of decay in living trees by means of the thulium x-ray unit. art. 37
Rate of decay in northern hardwoods following artificial inoculation with some common heartrot fungi. art. 223

REDMOND, D. R. art. 64
REINES, M. art. 70
Relation between site indexes of eastern white pine and red maple. art. 279
Relation of cubic-foot volume growth to stand density in young slash pine stands. The. art. 49
REMSON, IRWIN. art. 18
RICHARDSON, S. D. art. 174
Root regeneration of ponderosa pine seedlings lifted at different times of the year. art. 322
ROTH, LEWIS F. art. 182, 365
RUDINSKY, J. A. art. 259
SATTERLUND, DONALD R. art. 28
Sawfly cocoons. Weather, water levels and larch. art. 28
SCHAFFALITZKY DE MUCKADELL, M. rev. 412
SCHUBERT, GILBERT H. art. 322
Seasonal discoloration of Scotch pine in relation to microclimatic factors. art. 333
Seasonal variations in sugars of conifers with some observations on cold resistance. art. 56
Secondary phloem of Douglas-fir. The. art. 377
SHARPE, GRANT W. art. (rev.) 222
SHAW, R. H. art. 234
SILVERBORG, SAVEL B. art. 223
SMALL, JOHN A. art. 229
SMITH, FRANK H. art. 377
SMITH, J. HARRY G. art. 237
Some sampling attributes of the negative binomial distribution with special reference to forest insects. art. 397
Spacing and thinning. Comprehensive and economical designs for studies of. art. 237
Species hybridization in the white pines. art. 210
Spruce, black, to dwarfmistletoe infection. Brooming response of. art. 356
SPURR, STEPHEN H. art. (rev.) 157, 254, 364
Stand density in young slash pine stands. The relation of cubic-foot volume growth to. art. 49
Stem form and volume of Japanese larch in the Netherlands. rev. 254
STEVEN, H. M. rev. 157
STOLTENBERG, C. H. art. (rev.) 355
STONE, EDWARD C. art. 322
Sugars of conifers with some observations on cold resistance. Seasonal variations in. art. 56
Sweetgum blight as related to alluvial soils of the Mississippi River floodplain. art. 2
System for analysis of forest succession. A. art. 154
2,4,5-T tagged with carbon-14. Absorption rates of. art. 128
THIMANN, KENNETH V. rev. 291
Thulium x-ray unit. Radiographical determination of decay in living trees by means of the. art. 37
TOOLE, E. RICHARD art. 2
Tree radii and temperature. Winter changes in. art. 229
Tropical Silviculture. rev. 137
VAN SOEST, JAN. rev. 254
VITÉ, J. P. art. 259
WADSWORTH, FRANK H. art. (rev.) 137
WALKER, LAURENCE C. art. 128
Water conduction in conifers. Certain ecological and phylogenetic aspects of the pattern of. art. 259
WATERS, W. E. art. 397
Weather, water levels, and larch sawfly cocoons. art. 28
WILSON, CHARLES L. art. 114
Winter changes in tree radii and temperature. art. 229
Woodland vegetation and soils after spraying large amounts of waste water. Changes in. art. 18
WORLEY, J. F. art. 267
WORRELL, ALBERT C. rev. 355
WRIGHT, JONATHAN W. art. 210
ZIVNUSKA, JOHN A. For. Sci. Monog.1 (a separate)

Suggestions to Contributors

An article submitted for publication should be the best the writer is capable of producing, with all statements, tables, quotations, names and formulas verified before submission. The careful author will have his typescript reviewed by colleagues.

Articles should be typewritten, with 1½-inch margins, on one side only of white bond paper, size 8½ by 11 inches, or 8 by 10½ inches. Carbon copies are not acceptable. All copy should be double-spaced. Pages should be numbered consecutively, preferably in the upper right-hand corner. Only words intended to be set in italics should be underlined.

Material such as equations that exceed 42 spaces on the typewriter cannot be carried in a single line. Such material should either be set so that it can be broken into two or more lines, or should be presented in tabular form.

Tables

Each table should be typewritten on a separate sheet, given a title at the top, and should be numbered consecutively. Even if only one table is submitted, it should be designated Table 1.

Footnotes used in tables should be designated by numerals, never by asterisks or other typographical symbols. These footnotes should be typewritten as part of the table.

Illustrations and Figures

An illustration — whether a photograph, a line drawing, a map, or a graph — is designated as a figure. A caption should be submitted for each illustration, but the caption should be typewritten on a separate sheet.

All figures should be numbered consecutively. If only one is submitted it should be designated Figure 1. On the margin or back of each illustration should be written lightly in soft pencil the number of the figure, the name of the author, and an abbreviated title.

Photographs should be sharp and clear, printed on glossy paper. They should not be smaller than 4 by 5 inches. Sizes 5 by 7 inches and 8 by 10 inches are preferable. Photographs should never be rolled or bent. Care should be taken in fastening photographs with paper clips which often make indentations that show up in reproduction.

Drawings, maps, charts, and graphs are reproduced as line engravings. They should be at least twice as large as they are to appear when reproduced, and should be drawn in india ink on heavy white paper, or tracing cloth.

Footnotes

To indicate a footnote, place a superior figure after the word that refers to the note. Consecutive numerals should be used, never asterisks. Separate the footnote from the text by running a line about one inch inward from the left margin of the type.

Use footnotes to give credit to unpublished material and communications. If only a few references to literature are made (less than one per 1000 words), complete literature citations may be given in footnotes rather than in a separate listing.

Literature Cited

In FOREST SCIENCE practice, references to literature citations are designated by the author's name and year of publication inserted in parentheses at the appropriate place in the text. If there are more than two authors, list only the senior author's name in the text with the abbreviation *et al.* Example: (Smith *et al.*, 1954). Only published references should be given in *Literature Cited*. Periodical abbreviations should follow *Guide to the use of Forestry Abstracts*, Commonwealth Forestry Bureau, Oxford, England, 1950.

Nomenclature and Terminology

When a species is first mentioned in a paper its common name may be immediately followed by its italicized scientific name in parentheses, but this latter name need not be repeated.

As the authority for the exact spelling of tree names, FOREST SCIENCE follows *Check List of Native and Naturalized Trees of the United States (including Alaska)*, Agriculture Handbook 41, Forest Service, U. S. Dept. Agric., Washington, D. C., 1953.

For the spelling of other plant names, contributors should follow *Standardized Plant Names*, 2d Edition, J. Horace McFarland Company, Harrisburg, Pa. 1942.

Technical usage in forestry and allied fields follows *Forestry Terminology*, 3rd Edition, Society of American Foresters, Washington 6, D. C. 1958.

There are many style manuals available for the guidance of writers. One of the best is the *Style Manual* of the U. S. Government Printing Office, Washington 25, D. C. 1959.

Webster's *New International Dictionary* is the accepted authority for general spelling.